

CHANGES IN DETECTABILITY OF DIRECTION AND MOTION ASSOCIATED WITH
SACCADIC EYE MOVEMENTS

By

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The world is perceived to be stable, even though we move our eyes. Perceived stability is disrupted, however, if the eye is moved passively by gently pressing on one with a finger. The present series of studies explores the nature of perceptual stability during saccades, the kind of eye movement made when looking from one object to another. Saccades are high velocity eye movements; they are highly stereotypic and usually last less than 100 msec. They are interesting because they might be expected to disrupt perceptual stability, yet they do not.

The first study deals with changes in perceived direction associated with saccades. There are two theories concerning the role of a centrally originating corollary discharge in readjusting perceived direction. One theory states that perceived direction is readjusted continuously and slowly, while the other states that the readjustment is discrete and abrupt. Results from the first experiment contradict both theories, showing that perceived

direction is adjusted continuously and quickly. It was also found that perceived direction is readjusted slightly before the saccade begins.

The second study asks why the readjustment observed in the first experiment is not normally perceived as a motion of the world. Motion sensitivity was tested using a 2 cycle/° grating moved such that the patterns seen before and after the eye movement were identical. Velocity was 770°/sec; the extent of motion ranged from 0.5° to 8° (1 to 16 cycles). Thresholds for detecting motion during saccades were found to be about three times greater than thresholds during fixation. Moreover, the extent of motion at threshold was larger than the 2° eye movements used in this study.

The third study addresses the issue of stability of the world using postural stability as the dependent measure. The results are complex. It appears that some motion information during saccades is still obtained by the postural control system, although this information may not be enough for a characteristic response to be made.

Together these studies support the supposition that a corollary discharge may be an important mechanism for perceptual stability during eye movements.

CHAPTER I INTRODUCTION

To introduce the topic, try an experiment. First close one eye. Next, gently press the other eye through the lid, keeping the eye open and observe what happens. The world should appear to move in the direction opposite to the direction the eye rotates. Do not be terribly surprised if the world moves in the direction you press your eye, for some people the eye rotates against the direction the eye is pressed (Hill, 1984; Miller, Moore, & Wooten, 1984). Compare this situation to what happens when you look from one side of the page to the other. In this situation the world is perceived as stable, and yet, the displacement of the visual stimulation in the eye is, if anything, more drastic than what occurred when you pressed your eye. This simple experiment demonstrates how remarkable it is that we perceive the world as stable, especially in the face of eye movements. It also indicates that our perceptual systems must play an active role in this perceived stability.

One question that may arise is why the eye needs to move at all? That question can best be answered by a brief description of the anatomy and functioning of the eye. When light from an object enters the eye, the optical elements of the eye, the cornea and the lens, focus an image of that object onto the retina. The retina is a thin piece of tissue that lines the back of the eye, and it is in the retina that light energy is transduced or converted into nervous system activity. Eye movements are necessitated, in part, because only a small area of the retina, the fovea, that is capable of detailed vision. When

detailed inspection of an object is desired, the eyes must be directed so that the image of that object falls on the foveas of both eyes. When a person is looking at an object, it means that the object is imaged on both of his foveas.

One of the most common eye movements is the saccade. Saccades are executed when an observer looks from one object of regard to another or from one part to another part of the same object. They are conjugate eye movements; that is, the eyes move together. Saccades are also very stereotypic in that those of a given size and direction are very similar from one time to the next. They, also, can achieve extremely high velocities (Alpern, 1971; Carpenter, 1977). The duration of the vast majority of saccadic eye movements is shorter than the temporal integration period of the visual system, or the time period across which the visual system sums light energy. From this fact, it would be expected that saccades would be easily noticed, yet they are not. In fact, Dodge (1900) spent three years trying to train himself to reliably detect his own saccadic eye movements. After this extensive training, his ability to detect his own saccades was still no better than that of an untrained subject.

Two basic questions have been raised about why saccades are not easily noticed or detected: 1) Why is the image smear not noticed during a saccade? 2) What mechanism(s) is (are) responsible for the perception of a stable world both before and after a saccade occurs (Helmholtz, 1909/1962). The perceived stability of the world may seem an intuitively obvious event until two additional observations are considered. First, recalling the experiment used to introduce this paper, gently pressing the eye through the lid at the outer canthus, the world appears to move in the direction opposite to the rotation of the eye (Helmholtz, 1909/1962; Hershberger, 1984; Miller et al., 1984; Stark & Bridgeman, 1983). During both the eye press and the saccade, the pattern of

light stimulating the retina is very similar. Thus, it is apparent that the perception of a stable world is not inherent in the stimulation, *per se*, but relates in some way to the act of executing a saccade. The second observation, from studies of eyes paralyzed via either injury or appropriate medicine, reinforces the first. If a person with a paralyzed eye attempts to make a saccade, the world will seem to move or be displaced, this time in the direction of the attempted eye movement (Stevens et al., 1976). These two observations together reinforce the idea that the perceived stability of the world before and after saccadic eye movements results from some active mechanism.

Another way of describing these observations, is that during eye movements, there is spatiotopic stability in the face of retinotopic change. *Spatiotopic* refers to the coordinate system of the outside world. Eye movements do not interfere with our perceptions of this coordinate system while eye presses and attempting eye movements with paralyzed eyes do. *Retinotopic* refers to the coordinate system of the retina. The fovea is taken at the center of the retinotopic coordinate system. The relationship of retinotopic coordinates to spatiotopic coordinates is altered during an eye movement. Yet, this change does not disrupt the perceived stability of spatiotopic coordinates. This spatiotopic stability is the subject of the experiments discussed below (Chapters II, III, IV).

The rest of Chapter I will review and consider research pertaining to the question of why saccades are not easily noticed. Considerably more research has been conducted in an attempt to answer this question than in trying to understand the stability of perception around the time of saccades. Nevertheless, the efforts in this area have uncovered some mechanisms that are useful in understanding the question of perceptual stability.

Threshold Elevation During Saccadic Eye Movements

The first quantitative studies of reduced ability to detect visually presented stimuli during saccadic eye movements were done by Latour (1962) and Volkman (1962). Both researchers measured visual sensitivity by comparing thresholds during the saccading eye to thresholds for the fixating eye. In both cases, a decrease in sensitivity or elevated thresholds were observed when the saccading eye was compared to the fixating eye. Later research indicates that the reduction in visual sensitivity begins up to 100 msec prior to the onset of the saccade and lasts 160 msec after the saccade ends (Volkman, Schick, & Riggs, 1968). Volkman (1962), measuring the threshold for detecting a brief flash against a diffuse background, found a peak threshold elevation of 0.5 log units for the saccading eye relative to the fixating eye. This time course and magnitude of the reduction in sensitivity associated with saccadic eye movements, termed "saccadic suppression," is typical (see Matin, 1974; Volkman, 1976, 1986 for reviews).

Similar results have been obtained when measuring absolute thresholds (Volkman, 1962), incremental and decremental thresholds against a diffuse background (Riggs, Volkman, Moore, & Ellicott, 1982), and contrast sensitivity for gratings (Volkman, Riggs, Moore, & White, 1978). Moreover, similar findings have been obtained when studying blinks (Volkman, Riggs, & Moore, 1980) and vergence eye movements (Manning, 1986; Manning, & Riggs 1984). The only difference of note is that thresholds to increments from a steady background during blinks do not seem to be "suppressed" to as great a degree as decrements from the same background level (Riggs, White,

Manning, & Kelly, 1984; White, Krantz, Manning, & Moore, 1984). Factors that increase the amount of suppression that occurs during a saccade are increasing luminance, increasing the number of contours in the background, and increasing the size of the saccade (Brooks & Fuchs, 1975; Volkmann, Riggs, Ellicott, & Moore, 1981).

Mechanisms of Saccadic Suppression

Two classes of mechanisms have been proposed to account for saccadic suppression. These mechanisms can be broken down into those in which suppression arises as a result of retinal stimulation associated with the eye movement and those in which suppression arises extraretinally. The proposed mechanisms that arise as a result of retinal events are: 1) smearing of the retinal image as a result of the velocity of the eye movement and the temporal integration properties of the retina (Dodge, 1900; Matin, 1974) 2) metacontrast backward masking, where the clear image at the end of the eye movement blocks perception of the smeared image that resulted from the eye movement (Matin, 1974; Matin, Clymer, & Matin, 1972), and 3) shearing forces that arise in the retina as a result of the high velocity of the saccadic eye movement (Richards, 1968, 1969).

The extraretinal mechanisms can also be broken down into three types: 1) a feedback mechanism where saccadic suppression arises as a result of proprioceptive feedback from the extraocular muscles. This mechanism is also referred to as an inflow mechanism. 2) There is also the proposal that the command to move the eyes sends a corollary signal or discharge to the visual

system which may be involved in saccadic suppression (Helmholtz, 1909/1969). This mechanism is also referred to as an outflow mechanism. 3) Finally L. Martin (1976a) has proposed a mechanism that results from a combination of the two sources of information, referred to as a hybrid mechanism. Each potential mechanism will be discussed starting with the retinal mechanisms.

Retinal Image Smear

The high velocity of saccades has two effects upon the stimulation of the retina that fall roughly under the category of image smear. First, a stimulus is less effective during a saccade since each receptor receives less stimulation as the image of the stimulus sweeps past (Volkmann, 1986). Given that most saccades are completed within the temporal integration period of the eye (Bahill, Clark, & Stark, 1975), the reduction of the stimulus energy at each retinal location should reduce the effectiveness of the stimulus, that is, the change in luminance across a contour should be reduced towards threshold.

The second impact on vision that the high velocity of the eye could have is best described via an example. If a camera is swept across a visual scene with the shutter held open, the resulting exposure will be a sort of temporal average of the light distribution across the visual scene. Such an exposure will not reveal any clear details on the photograph. Again, since saccades are usually completed within the time period covered by Bloch's Law, which describes the temporal integration properties of the eye (Bahill, Clark, & Stark, 1975; Cornsweet, 1970), a similar type of temporal average is performed by the visual system which can reduce the sensitivity of the visual system. That image smear plays a role in saccadic suppression is supported by observations

that the degree of suppression increases as the complexity of the scene and luminance is increased, both factors that would increase the amount of image smear present during a saccade (Brooks & Fuchs, 1975). Moreover, elevation of visual thresholds has been observed when the visual scene is moved and the eye is kept still (Brooks & Fuchs, 1975).

The influence of image smear, *per se*, on saccadic suppression was investigated directly by Volkmann et al. (1978). In their experiment, they controlled image smear during both fixations and saccades. As expected, increasing image smear on the retina increases the contrast threshold for the detection of a grating, but the effect was much greater for the fixating eye than for the saccading eye. The lowest threshold found for the detection of the grating during a saccade, when image smear was near minimum, was still greater than the greatest threshold found for the fixating eye, with the maximum image smear used. Volkmann et al. (1978) concluded that image smear, *per se*, is not a sufficient factor to completely account for the threshold elevations observed to accompany saccades.

Metacontrast Backward Masking

Visual masking can be described as the altering of the detectability of one briefly presented stimulus (the target) by the presentation of another briefly presented stimulus (the mask) (Breitmeyer, 1984; Breitmeyer & Ganz, 1976). The use of the term "masking" refers to the usual finding that the ability to detect the target is usually reduced by the presence of the mask. If the mask precedes the target in time, the masking situation is referred to as forward masking; conversely, when the mask follows the target in time, the situation is referred to as backward masking. The temporal offset between the

target and mask is referred to as stimulus onset asynchrony (SOA) where the time the target is presented is the reference time or a time of 0. Positive SOAs refer to backward masking and negative SOAs refer to forward masking.

Visual masking can be grouped into two basic types, labelled Types A and B. Types A and B refer to the existence of two different empirical functions relating SOA and the amount of masking observed (Breitmeyer & Ganz, 1976). The Type A masking function has the greatest magnitude of masking when the SOA is 0 msec. As the SOA is increased in either the positive or negative direction, the amount of masking observed reduces quickly and symmetrically about an SOA of 0 msec. By the time the SOA is 200 msec positive or negative, the degree of masking of the target is negligible (Breitmeyer, 1984; Breitmeyer & Ganz, 1976). The stimuli that produce Type A masking have overlapping contours. Such masking is referred to as either masking by noise, if the target and mask bear no structural resemblance, or masking by structure, if elements of the target are used to construct the mask, though under some circumstances masking by structure will produce Type B masking (Breitmeyer & Ganz, 1976).

With Type B masking, the degree of masking is not symmetrical around an SOA of 0 msec. Backward Type B masking produces a much greater degree of masking than forward Type B masking. The greatest degree of masking occurs when the mask is presented 100 to 200 msec after the target. For forward Type B masking, the masking is greatest with an SOA of approximately -50 msec. The typical stimulus situation that leads to backward masking employs a stimulus in which the target and mask do not have overlapping contours (Breitmeyer, 1984; Breitmeyer & Ganz, 1976). Type B backward

masking is also referred to as metacontrast, which is the term that will be used throughout the rest of the present paper.

It is the fact that metacontrast does not require overlapping contours that has made this phenomenon attractive as a potential mechanism of saccadic suppression to the almost complete exclusion of consideration of other forms of masking (Breitmeyer & Ganz, 1976; Dodge, 1900; Matin, 1974). The hypothesis states that the pattern of stimulation on the retina that results from a saccade resembles the situation used to obtain metacontrast. Specifically, the clear image present after the eye movement ends has appropriate characteristics (spatially and temporally) to mask the perception of the smeared image that occurs during the eye movement.

Matin, Clymer, and Matin (1972) provided an elegant demonstration of the role that metacontrast may play in saccadic suppression. In their experiments, subjects viewed a vertical slit displayed during an horizontal saccade. If the slit was removed from the subject's view prior to the end of the saccade, the subject would report the perception of a smeared streak, but if the slit was left on briefly after the end of the saccade the perception of smear would be reduced or eliminated. It is important to note how this experiment fits the metacontrast paradigm. The clear image of the slit followed the smeared image, and, more importantly, the clear image of the slit was not on the same retinal location as the smeared image.

The role of metacontrast in saccadic suppression is further supported by the observations that suppression increases as luminance and scene complexity increases (Brooks & Fuchs, 1975). Elevations of visual thresholds can be found when the eye is still and the surrounding scene is moved (Brooks & Fuchs, 1975). These observations taken together have led E. Matin (1974) to

propose that metacontrast masking exists to serve in saccadic suppression. Yet, note that for metacontrast to operate efficiently, both sufficient luminance and a contoured visual scene are needed. Thus, metacontrast is limited in the range of conditions that it can effectively contribute to saccadic suppression (Volkman, 1976;1986), though this range of conditions covers most situations encountered.

Up to now, all other forms of masking have been ignored as potential contributors to saccadic suppression. While they have not been given much treatment in the psychophysical literature (Matin, 1974; Volkman, 1986), some of the physiological evidence to be discussed below seems to suggest some role for both forward and backward Type A masking. The clearest example of a potential role for Type A masking was shown by Judge, Wurtz, and Richmond (1980). They found cells in the striate cortex of monkeys that showed an attenuated response to a stimulus that moved across the receptive field at saccadic velocities when another discrete stimulus either preceded or followed the target stimulus. The masking was greatest with an SOA of 0 msec and was nearly absent when the SOA is either a positive or a negative 50 msec. The masking stimulus was also presented in the receptive field. The findings were replicated psychophysically with human subjects (Judge, Wurtz, & Richmond, 1980) and in cells in the superior colliculus (Wurtz, Richmond, & Judge, 1980). Interestingly, metacontrast has yet to be clearly observed in the single unit recordings.

Retinal Shear

The final mechanism proposed that depends upon peripheral events is the retinal shear hypothesis of Richards (1968, 1969). According to this

hypothesis, the great angular acceleration within the eye, coupled with the different moments of inertia within the eye tissues, leads to shearing forces within the retina, and it is these shearing forces that cause suppression. This hypothesis has rarely been investigated directly but several observations argue against this factor being a major contributor to saccadic suppression. First, major supplemental hypotheses are required to account for suppression prior to and following the eye movement. For example, both a neural delay to account for suppression prior to the eye movement and a prolonged settling time to account for suppression following the saccade are required. Moreover, threshold elevations resembling saccadic suppression in terms of magnitude and time course have been observed to be associated with blinks and vergence eye movements (Manning, 1986; Manning & Riggs, 1984; Volkmann, 1986; Volkmann, Riggs, & Moore, 1980). In neither case are the shearing forces likely to be as large since the accelerations of the eye are small. Finally, measurements of saccadic suppression with psychophysical techniques led to the observation that the magnitude of suppression increases as saccade size increases (Volkmann, Riggs, Ellicott, & Moore, 1981), which is consistent with the retinal shear hypothesis since suppression increases as acceleration, and presumably the magnitude of the shearing forces, increase. But Krantz and White (in preparation) found the opposite trend using body sway as a measure, a finding counter to the retinal shear hypothesis. If the retinal shear hypothesis were correct, increasing the acceleration of the eye should, at least, not lead to a decrease in suppression.

Inflow or Feedback Extraretinal Mechanism

The inflow model for saccadic suppression is attributed originally to Holt (1903), who proposed that saccadic suppression was caused by feedback signals from the extraocular muscles. Several sources of information argue against a pure inflow model as an explanation of saccadic suppression. First, the time course of saccadic suppression is inconsistent with the feedback idea because saccadic suppression begins long before the onset of the feedback signal from the eye muscles. Additionally, the observed motion of the world during an eye press, when feedback from the eye muscles is presumably present, also seems to be inconsistent with feedback theories of saccadic suppression. It is also interesting to note that an afterimage will not appear to move during an eye press (this observation works best when the eye is closed to avoid any induced movement of the afterimage moving relative to the background) (Hershberger, 1987). In this case, the feedback signal should be present to indicate the eye moved while the stimulus remained still on the retina. The sum of these signals should produce apparent motion of the afterimage if feedback were involved in perceptual stability. The observed displacement of the world during paralyzed eye experiments also argues against the inflow model. Since the eye does not move and no feedback can occur, then feedback models should predict that the world should not appear to move during saccadic eye movements. The fact that the world does appear to move in this case suggests that some other extraretinal source must be involved in saccadic suppression.

If feedback were a good source of extraretinal information for saccadic suppression, then feedback would be expected to be a major contributor to eye position sense. Eye position sense refers to the sensory impression of the

direction of the eye relative to the head. In the case of human eyes, afferent (feedback) information apparently provides only a coarse input to the eye position sense. Human extraocular muscles are amply supplied with sensory endings (Cooper, Daniel, & Whitteridge, 1955; Matthews, 1972; Sherrington, 1897; Wolter, 1955), including a similar quantity of muscle spindle organs sensitive to stretch in other skeletal muscles (Cooper, Daniel, & Whitteridge, 1955; Matthews, 1972). Yet, what role these sensory organs play in an eye position sense is presently unclear. Their contribution to an eye position sense would seem to be minimal as noted from the observations in the preceding paragraph and from the finding that the eye can be displaced passively to a large extent without the subject being aware of such a displacement (Brindley & Merton, 1960; Merton, 1964; Skavenski, 1972). The area that the eye can be passively moved without the subject being aware of the movement extends to at least 10 degrees to either side of fixation, and this is only for practiced subjects (Skavenski, 1972). With unpracticed subjects, displacements of up to 40 degrees to either side can go unnoticed (Brindley & Merton, 1960).

Outflow of Feedforward (Corollary Discharge) Extraretinal Mechanism

The most popular model for saccadic suppression that arises from extraretinal sources is the corollary discharge. The initial model of the corollary discharge (Sperry, 1950) was based upon Helmholtz's (1909/1962) idea of "effort of will." Basically, the model states that the motor system sends a copy or *effereenz copie* of the motor command to the visual system to "inform" it of the perceptual effect of the intended motor act (Held, 1961; Holst, 1954). This model seems corroborated by studies of perceptual rearrangement as long

as the interaction of the corollary discharge with visual signals is assumed to be to some degree plastic (Held, 1961). The issue of plasticity will be discussed in greater detail below.

No matter what form the corollary discharge takes, psychophysical evidence seems supportive of some role for a centrally originating corollary discharge being involved in saccadic and other forms of suppression. In many studies, stimuli are presented briefly on diffuse backgrounds to avoid potential effects of image smear and masking (Volkman, 1962; Volkman, Schick, & Riggs, 1966). To rule out potential masking from the slightly visible contours of the face (e.g., the nose), Riggs and Manning (1982) placed cut out ping-pong balls, effecting a *ganzfeld*, close to the eyes for more complete removal of contours and found the typical amount of suppression. Perhaps the most impressive support for a corollary discharge being involved in saccadic suppression comes from Riggs, Merton, and Morton (1974) who used visual phosphenes in complete darkness and still found saccadic suppression of 0.4 log units.

Another source of information about any role the corollary discharge might have in saccadic suppression is from physiological studies of the activity of the visual system during saccades. Discovering evidence at the physiological level consistent with a corollary discharge has proven to be a difficult task. Much of the difficulty may have arisen because the operation of the corollary discharge may be more subtle and complex than at first had been thought.

A study by Richmond and Wurtz (1980) does find support for such a function of the corollary discharge in the superior colliculus of the rhesus monkey. They found cells in the superficial layers of the superior colliculus,

the "visual" layers (Schiller, 1972), that showed a reduced sensitivity to visual stimulation around the time of saccades. They determined that the reduction in sensitivity was due to a centrally originating corollary discharge, because the magnitude of the reduction of sensitivity was the same in light and dark conditions and after retrobulbar block. Since the reduction in sensitivity occurred in darkness, masking and smear were eliminated as potential factors. The retrobulbar block eliminated feedback from extraocular muscles, so inflow information was not available (Richmond & Wurtz, 1980).

Judge et al. (1980) did not observe such a suppression of response of cells in the striate cortex of rhesus monkeys. Yet, other investigators have found some evidence of suppression of visual responses during saccadic eye movements along the primary visual pathways. Creutzfeldt, Noda, and Freeman (1972) have found that some cells in the lateral geniculate nucleus (LGN) are suppressed by saccades. The observed suppression did not depend upon the presence of visual stimulation but was only related to the presence of a saccade. Bartlett, Doty, Lee, and Sakakura (1976) observed suppression of visual evoked potentials recorded in the optic radiations and striate cortex. This suppression continued in the dark and was replaced by facilitation 100 msec after the end of the saccade. Yet, these findings do not represent the entire pattern of physiological results around the time of saccades. In the same report, Creutzfeldt et al. (1972) found some cells in the striate cortex being facilitated, while many cells do not respond at all during an eye movement.

There is a sizable negative potential observed in the LGN during saccades that seems to have an extraretinal origin. The negative potential during saccades seems to be related to the pontine-geniculo-striate (PGO)

potential first observed during rapid eye movements in sleeping subjects (Singer, 1976). This negative-going potential does not seem to be inhibitory but seems instead to function to release inhibition within the lateral geniculate nucleus (LGN) of the thalamus, the structure where the neurons leaving the eye synapse with neurons that will carry the information to the cortex. During normal viewing of a complex visual scene, substantial inhibition within several levels of the visual system develops (Coren, Porac, & Ward, 1984). This inhibition is usually thought to be essential to normal viewing. However, to be useful, the pattern of inhibition must be related to the pattern of contours in the environment (lateral inhibition, Bekesy, 1967; Cornsweet, 1970). This pattern of inhibition at the time of a saccade would not be related to the new visual scene present after an eye movement and could disrupt the clear viewing of the new scene. It has been proposed (Singer, 1976) that the function of the PGO wave is to release the visual system from this build up of inhibition so that the new scene at the end of the saccade can be efficiently processed. Such a function seems essential and may well operate along side the suppression of visual responsiveness during the saccade. Thus, physiological studies suggest that a corollary discharge may both suppress visual sensitivity during a saccade and prepare the central pathways for processing the next clear image. It should be noted that both facilitation and inhibition observed at one level of the nervous system may ultimately have the opposite effect at another level of the nervous system, so such conclusions should not be held to be firm.

6) Matin's hybrid extraretinal mechanism

In 1976, L. Matin (1976a; see also L. Matin, 1982) published an article in which he tried to resurrect an inflow theory of saccadic suppression by combining it with outflow information. Basically, the theory proposes that feedback from the extraocular muscles is the primary extraretinal signal, but that this feedback is altered by centrally originating signals. The proposal states that the corollary discharge exists, but acts only as a gate for inflow information.

This proposal allows him to account for the observations from eye press and paralyzed eye experiments in a manner similar to how corollary discharge explanations account for these observations. In fact, he admits that data from these two sources do not discriminate between the two hypotheses. Thus, the hybrid model seems to be counter to the usual scientific tenet of parsimony.

In addition, an observation by Stevens et al. (1976) seems contrary to Matin's hypothesis. Within the context of the hybrid theory, feedback information must be able to leave the eye for the illusions observed during eye presses and paralyzed eyes to occur. In the last experiment in Stevens et al. (1976), a retrobulbar block was used which prevented both motor commands from reaching the eye and feedback information from leaving the eye. Still, they observed that the world appeared displaced after an attempted eye movement, as measured by the presence of the subject pointing beyond objects in the direction of the attempted saccade and subject reports. In addition, the poor feedback mechanisms in the eye make even gated inflow information about eye position of a dubious quality (Brindley & Merton, 1960; Steinbach, 1987).

Summary

This first chapter has heavily emphasized the literature on saccadic suppression from both psychophysical and physiological research and thus has emphasized the first of the two questions related to vision around the time of saccadic eye movements: why the smear that results from executing a saccade is not noticed. This research has primarily focused on elevations of some type of threshold during the saccading eye as compared to the fixating eye. Suppression is incomplete, typically measured at about 0.5 log units (E. Matin, 1974; Volkmann, 1976; 1986). The actual degree of suppression depends upon numerous factors including the size of the eye movement, luminance, and complexity of the visual scene (Brooks & Fuchs, 1975; Volkmann et al., 1982).

This observed suppression is best accounted for by three factors working in conjunction. One important factor seems to be visual masking (E. Matin, 1974). Usually metacontrast masking is invoked where the clear image at the end of the saccade masks perception of the smeared image during the saccade. Yet, some physiological evidence suggest that both forward and backward Type A masking may be involved. One limiting factor about masking is that it depends upon sufficient luminance and the presence of contours to be effective. Retinal smear is another mechanism that could act to cause saccadic suppression (Volkmann et al., 1978). The major extraretinal source of saccadic suppression appears to be a centrally originating corollary discharge which can operate under any visual condition (Volkmann, 1976, 1986). Other potential extraretinal sources of saccadic suppression, inflow and L. Matin's

(1976a) hybrid mechanism, do not seem to adequately account for all of the eye press and paralyzed eye data. While Richard's (1968, 1969) retinal shear hypothesis has not been greatly examined, it has difficulty with suppression observed during blinks and vergence eye movements and the decrease in "suppression" for larger saccades when body sway is measured (Krantz & White, in preparation).

The next chapter will discuss previous research on the second question of how the world maintains a perceptual stability around the time a saccade occurs. After this discussion, the first experiment will try to resolve some conflicts in the data gathered to date.

CHAPTER II
EXPERIMENT 1:
SACCADIC EFFECTS ON LOCALIZATION

Previous Research

The importance of studying what happens to the sense of direction during a saccade is related to the second question mentioned in the introduction. Namely, why the world is perceived to remain stable during a saccadic eye movement. Principally, the eye press experiments and paralyzed eye experiments seem to suggest that some sort of centrally originating corollary discharge seems to be involved. This idea was originally espoused by Helmholtz (1909/1960) and expanded by Holst (1954) and Held (1961). In general, the hypothesis states that any intended movement leads to a corollary signal that counters the sensory signal which results from the movement and which might indicate motion of the world. In effect, the sensory signal indicating that the world is moving is cancelled, leaving the perception of stability. Note that in this situation, a corollary discharge does not as much inhibit visual functioning as it selectively cancels incoming sensory information that is expected to be the result of the intended movement.

L. Matin and his colleagues (Matin, 1972; Matin, Matin, & Pearce, 1969, 1970; Matin & Pearce, 1965; Matin, Pearce, Matin, & Kibler, 1966) were the first to investigate these ideas directly as they related to

saccadic eye movements. In their paradigm, they presented briefly flashed stimuli either just before, during, or after the saccade and their subjects were asked to judge whether the flashed stimulus was to the left or to the right of the initial fixation target which had been removed at least 500 msec earlier. Their results indicated a slow readjustment of perceived direction, consonant with the change of eye position, beginning well before the saccade and lasting about 300 msec after the saccade. From their data, Matin et al. (1969, 1970) argue that the corollary discharge portion of perceptual readjustment takes up to 0.5 seconds to complete. Another feature of these data to note is the wide intersubject variability in their judgements before, during, and after the saccades. Such intersubject variability is unusual in a large proportion of psychophysical studies.

Matin observed another pattern of results when judgements of direction were made to a briefly presented stimulus presented earlier in the same saccade (Matin, 1976b). Matin (1976b) refers to this study as the two-flash paradigm. In this case, perceived direction seemed to be locked to the same retinal location of the first flash, regardless of its spatial direction, until after the end of the eye movement when a more rapid readjustment of perceived visual direction occurs. Matin (1976b, 1982) argues that these results do not reflect the operation of the corollary discharge but the effects of visual persistence of the first flash overriding the corollary discharge.

By discounting the results for the two-flash paradigm, L. Matin uses the results from the first experiments to argue that the corollary discharge is a slow signal. Specifically, he argues that the corollary discharge takes a relatively long time to readjust perceived direction to

match the new spatial coordinates resulting from the eye movement. Thus, the corollary discharge is not the primary factor in perceived stability around the time of eye movements. In fact, he argues that visual context, even as primitive as a single dot fixed in space, can provide sufficient information to readjust the perception of direction (Matin, 1972, 1976b).

The conclusions that Matin draws from his data could be incorrect for two basic reasons. First, Matin (1976b; Matin et al., 1969) does not provide any evidence to support the supposition that the persisting image of an object controls the perception of the direction of that object. His argument is based on the observation simply that persistence exists (Bowen, Pola, & Matin, 1974). The possibility remains open that persistence may not explain the results from the two-flash paradigm. If this is the case, then there is no *a priori* reason to believe that the data obtained when judgements were made to the initial fixation target are any more representative of the action of the corollary discharge than data from the two-flash paradigm data.

In fact, it is possible that the temporal separation between the initial fixation target and the flashed stimulus whose direction is to be judged in the original experiments (Matin et al., 1969, 1970) could have been responsible for the pattern of results observed. Since, the judgements of direction are made to a location in space that is only remembered, errors in memory could have contaminated the results in these experiments, perhaps explaining the wide intersubject variability (Hershberger, 1987; Skavenski, 1976; Skavenski, & Steinman, 1970). Such considerations lead to difficulty in interpretation of Matin's data.

Hershberger (1987) advanced a faulty-memory explanation to account for the data Matin et al. (1969, 1970) observed, but only for the data following the saccade. The linear trend in the changes of judged direction following the saccade fits Skavenski's expectancy for the pattern in the data if memory were to account for the results.

Hershberger (1987) does not use a memory explanation to account for the results Matin et al. (1969, 1970) obtained for changes in perceived direction prior to the saccade for two reasons. First, the flashes are closer in time to when the initial fixation target was removed, and the eye has not moved, so memory for the location of the initial fixation target should not be as much a problem. Secondly, the curvilinear trend in the data does not fit with Skavenski's (1976) expectation of the linear trend the data should take if memory is the explanation.

Hershberger (1987), instead, finds the pattern of results for flashes presented prior to the saccade consistent with his own model of the readjustment of the perception of direction around the time of saccades. His model includes von Holst's (1954) contention that the efference copy or corollary discharge is present and gives highly accurate information about the position of the eye at any moment, but this signal is not used when making psychophysical judgements. Instead, he proposes that there is also an efference copy (Hershberger, 1976, 1987) which he conceives of as a reference signal indicating where the eye will be after the end of the eye movement. The sense of "copy" used in the term "efference copy" is something to be duplicated or matched, whereas "copy" in the term "reference copy" has the sense of something that is itself a duplicate. The efference copy serves as a reference signal that the eye movement mechanism attempts to match

such that the eye movement sequence is complete when the efference copy is the same as the afference copy.

Hershberger's (1976, 1987) model of the perception of direction around the time of saccadic eye movements relies on the validity of Robinson's (1975, 1987) model of saccadic eye movements. Unlike typical models of the control of saccadic eye movements (Carpenter, 1977; Clark & Stark, 1974), Robinson proposes that saccades are not ballistic, nor is eye position sampled around the time of saccades, as opposed to continuously during smooth pursuit movements. Robinson (1975, 1987) proposes that eye position is continuously monitored even during saccades and that saccades are even mutable during their course. He argues that since the latency to execute saccades is long relative to the time it takes a normal saccade to be completed (Alpern, 1971), it only appears that saccades are ballistic. In fact, Robinson believes that the control signal used to generate saccades, and all eye movements, is derived from a signal that is proportional to the final position of the eye (an afference copy?). Given this model of saccadic eye movements, it seems more reasonable to propose some sort of reference signal against which current eye position is compared. If saccades are truly ballistic then eye position would not need to be monitored during a saccade.

Using Robinson's (1975, 1987) model of saccadic eye movement, Hershberger (1987) proposes that the afference copy controls the perception of direction as measured by psychophysical techniques. Since the reference signal, the afference copy, is present prior to the execution of the saccade, perceived visual direction is proposed to shift in the direction of the saccade by the size of the intended eye movement prior to the eye movement. Hershberger (1987) makes a supplementary

addition to his hypothesis to account for the curvilinear nature of the data of Matin et al. (1969, 1970) for judgements of direction prior to the saccade. To explain these data in a manner consistent with his theory, Hershberger proposes that the time that the afference copy takes effect and controls judgements of direction is variable with respect to the onset of the saccade. Thus, as the onset time for the saccade nears, the probability that the afference copy has been set up and is now controlling "conscious" judgements of direction increases. In this manner, the curvilinear nature of Matin et al.'s (1969, 1970) data can be accounted for.

The Present Study

The present study was designed with two purposes in mind. First, it seems important to test directly Matin's (1976a) contention that the pattern of results obtained from the two-flash paradigm was due to visible persistence (Coltheart, 1980). One way to test this hypothesis is to minimize the time interval between presentations of the stimuli used to judge direction while also reducing the possible effects of visible persistence. The present study will therefore minimize visible persistence by making all the stimuli decrements from a background luminance, which leads to far less persistence. To further reduce the amount of visible persistence from the stimuli against which direction is to be judged, these stimuli will be left on for at least 2.5 seconds. Increasing stimulus duration tends to reduce the persistence of the stimulus following its offset (Coltheart, 1980).

Still, a simple replication of Matin et al.'s (1969, 1970) paradigm will not be able to address Hershberger's (1987) hypothesis. If Hershberger's proposal is correct, then judgements of visual direction for stimuli presented prior to saccade onset should break down into two distributions. One distribution, representing judgements made prior to the afference copy being present, should center on the actual position of the reference target (the initial fixation target in Matin, Matin, and Pearce's experiments). The other distribution, representing judgements made after the afference copy is present should center around the position the reference target would occupy on the retina after the saccade was executed. In other words, these judgements should be shifted in space with the same direction and size as that of the upcoming saccade.

In Matin, Matin, and Pearce's original experiments, the above proposal could not be disproved. Yet, a minor adjustment to the stimulus situation would allow for judgements contrary to or consistent with Hershberger's model to be observed. To accomplish this aim, a stimulus will be placed halfway between the initial fixation target and the saccade target stimulus, and judgements of the position of the test flash will be made relative to the middle stimulus (see Figure 1).

Four, instead of two, responses are now possible. A judgment of "far right" indicates that the test flash appeared to the right of all three initial stimuli. A judgment of "right" indicates that the stimulus appeared between the rightmost target and the middle target. Judgements of "left" and "far left" have comparable meanings as presented in Figure 1. Critical target flashes to test Hershberger's

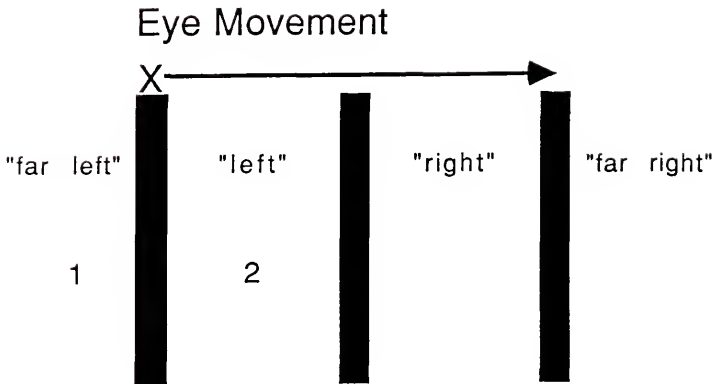


Figure 1. Stimulus arrangement used for Experiment 1. The eye movement is from the left outer target to the right outer target after the targets are removed. Judgements of the direction of stimuli flashed at locations 1 and 2 are critical for Hershberger's hypothesis. See text for an explanation.

hypothesis will be presented in locations 1 and 2 as shown in Figure 1. To understand the following discussion, it is important to note that all target flashes will be presented after the three initial stimuli are removed, and that all saccades are to the right. This second point is important as perceived direction should shift to the right, if perceived direction anticipates the saccadic eye movement. Prior to the saccade, a test flash presented in location 2 should *not ever* be judged to be "right" because the hypothesized afference copy leads to a discreet readjustment of judged position having the extent of the intended saccade. Either the target presented at location 2 should be judged to be "left" (before the perceived direction shifts) or "far right" (after the perceived direction shifts). Judgements of "right" to test flashes presented in location 2 indicate a shift in perceived direction, but this shift is *less* than the extent of the intended saccade. Thus, a judgement of "right" under these circumstances is inconsistent with Hershberger's hypothesis. Using the identical line of reasoning, under Hershberger's hypothesis, a stimulus presented in location 1 prior to the saccade should be judged either "far left" or "right," but not "left."

Method

Subjects

Three male subjects, volunteers, were run in this experiment. Their ages were 24 to 30 years old, and all had normal acuity.

Apparatus

The experiment was run on a Commodore 128 microcomputer. The computer presented stimuli, controlled and measured timing, collected subjects judgements and analyzed the data. Data were stored on a disk and analyses were performed off-line. The stimuli were presented on a Magnavox RGB Monitor 80 (Model #CM8562), using the green phosphor only. The decay of the phosphor was measured to be 4 msec to 10% of the original luminance. The light color reflective case of the monitor was masked off to flat black to reduce stray light on the stimuli.

The monitor screen was viewed through a high powered cylinder lens placed 24 inches (60 cm) from the face of the screen. Viewing was accomplished by placing the right eye of the subject just behind the lens (Figure 2). The effect of this optical arrangement was to cause a vertical integration of the light across the screen. For example, a black square presented against a white background would be seen as a vertical gray bar the width of the black square but extending vertically the entire field of view. With this arrangement, the vertical position along the screen raster could be used to time stimulus presentations for shorter periods of time than the typical screen frame (16.67 msec).

Saccadic eye movements were detected using an amplified electrooculogram (EOG). Appendix A contains a description of the amplifier and trigger device used. The amplified EOG signal was fed into a level detector that upon the detection of a rapid voltage change associated with saccades, sent a pulse to the Commodore 128 microcomputer to generate an interrupt so the computer would record the time of the saccade onset. The interrupt could be detected with an

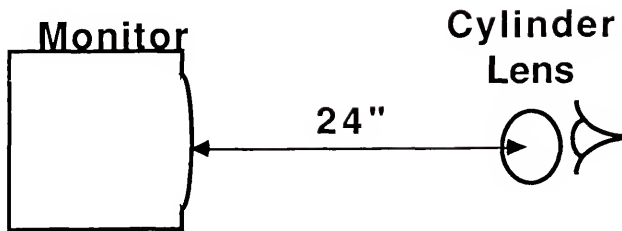


Figure 2. Optical placement of the monitor, cylinder lens and subjects right eye in Experiment 1.

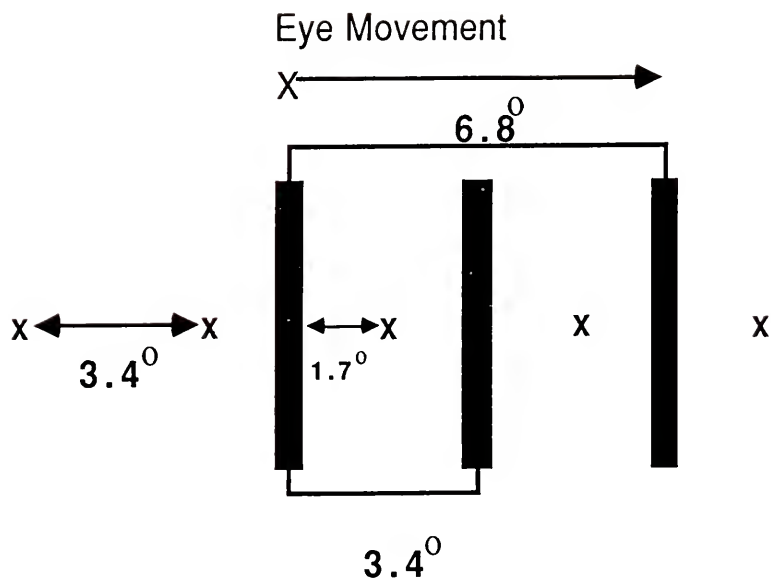
accuracy of 65 microseconds. The amplified EOG and trigger pulse were also fed into and displayed on a Techtronix Oscilloscope for online monitoring.

Procedure

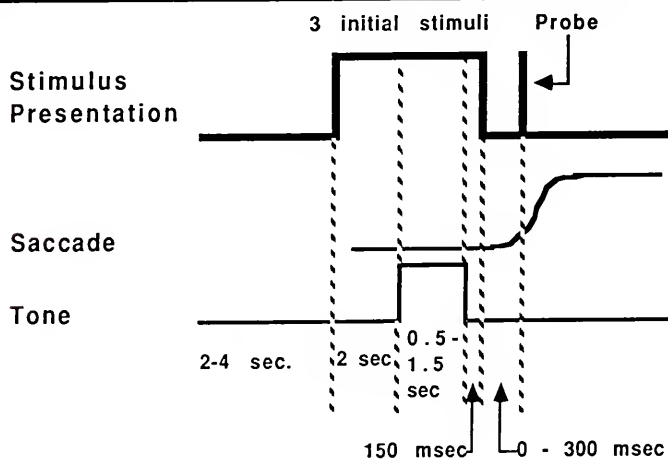
All of the stimuli used were 25' of visual angle wide. Each subject participated in at least 1000 trials, across several sessions lasting about 2 hours each. The EOG electrodes were placed bitemporally with a ground electrode placed on the left mastoid bone, just behind the ear.

Subjects began every trial by pressing a button on a joystick. This button press initialized a variable delay period of 2 to 4 seconds. Then the three initial stimuli were presented (Figure 3). Subjects were instructed to fixate on the stimulus to the left. The stimulus to the far right was the saccade goal, indicating a saccade of 6.8°. The middle stimulus is placed exactly halfway between the other two targets. Then, 2 seconds after the three initial stimuli were presented, a tone was sounded for a duration ranging from 0.5 to 1.5 seconds. The subject was instructed to execute the saccade to the far right stimulus when the tone was turned off. The three initial stimuli were removed 150 msec after the end of the tone.

The flashed probe stimulus was presented with a variable delay of 0 to 300 msec following the offset of the three initial stimuli. This variable timing allowed the flashed probe stimulus to be presented before, during and after the saccade had occurred. The time when the probe stimulus occurred relative to the saccade onset was determined by the computer which kept track of when the probe stimulus was presented and when the saccade onset was detected.



(a)



(b)

Figure 3. (a) Stimulus arrangement presented to the subject in Experiment 1. The "X"s indicate the locations used to flash the test probe stimulus. (b) The timing of events in a single trial in Experiment 1.

The position of the flashed probe stimulus was also variable, being presented in 3.4° steps starting 5.1° to the left of the fixation stimulus (the leftmost of the three initial stimuli) and ending 1.6° to the right of the saccade goal (the rightmost initial stimulus). Thus probe stimuli were presented to the left of the fixation stimulus, halfway between the fixation stimulus and middle stimulus, and halfway between the middle and saccade goal stimulus as well. Probe stimulus positions are indicated by X's on Figure 3.

After the end of every trial, the subject was instructed to make a judgement of the position of the flashed probe stimulus relative to the middle initial stimulus. Judgements of "far left" were to indicate that the subject perceived the probe stimulus to be to the left of where all three initial stimuli were located, "left" indicated the subject perceived the probe stimulus to be between the left fixation and middle initial stimuli, "right" indicated that the probe stimulus appeared between the middle and saccade target initial stimuli, and "far right" indicated that the probe stimulus appeared to the right of all three initial stimuli. An experimenter entered the judgement in the computer for storage on disk. The experimenter also monitored the EOG and trigger signals on the oscilloscope. If there was either a false trigger or if the probe stimulus was not perceived (subjects were encouraged to guess), the experimenter rejected the trial which was signaled to the subject.

The first two experimental sessions began with 10 practice trials which were identical to experimental trials except that the data were not stored on the disk. Sessions were not run to collect a predetermined amount of data but instead for a period of approximately 2 hours. The

session could be terminated sooner if the subject requested. Breaks were at the subjects discretion with at least one break after an hour.

Data Analysis

The times when the stimulus probe occurred relative to the onset of a saccade were grouped into 25 msec bins relative to the time of the onset of the saccade to give more stability to the data. The onset of the saccade was the center time for the 0 msec time bin. Positive times indicate that the probe stimulus occurred after the onset of the saccade. Within each time bin, the data were grouped by the position of the probe stimulus. Within the positions the data were also grouped by the judged position of the probe stimulus. Thus, in each time bin there were 20 groups of judgements (5 probe stimulus positions x 4 judgements). This data arrangement was used for the analyses described below.

Results

In order to compare the present results with Matin's earlier reports (Matin, 1972, 1976a; Matin et al., 1969, 1970), the point of subjective equality (PSE) was determined for the position of the probe stimulus relative to the middle initial stimulus at each of the 25 msec intervals. To make the data more similar, judgements of "left" and "far left" were grouped together for the present analysis as "left", and judgements of "right" and "far right" were grouped together as "right". The PSE was calculated as the probe position where subjects responded "left" on 50% of the trials. If no probe position was at exactly the 50%

position, a linear interpolation was made between the two flash positions that bounded the 50% position.

Figure 4 shows the calculated PSE in terms of spatiotopic coordinates for probe position as a function of the time relative to saccade onset. On Figure 4, the 0° location refers to the spatiotopic location of the middle initial stimulus. The three panels report data separately for each of the three subjects. Four features of the data are worth noting. Prior to saccade onset, all three subjects are reasonably accurate in their judgements of direction, as indicated by PSE near 0° . Secondly, all three subjects make errors in judged location in the direction towards the left ($PSE < 0$) near the time that the saccade begins. This would be consistent with perceiving that the eye has already moved to some extent to the right, the direction of the saccades in this experiment. The third feature is the tendency for judgements of direction to be more accurate during and shortly after the onset of the saccade. Typical 6.8° saccades take approximately 35 msec (Bahill, Clark, & Stark, 1975), so the 25 and 50 msec bins are important for this observation. The final feature is the breakdown of consistency of judged direction across subjects after the saccade has ended (bins 75 msec and greater). Two subjects judge the stimulus to be too far to the left (negative PSE's of up to 3.5°), while one subject (CBW) remains highly accurate in his judgements (PSE's near 0°).

There are several important differences between the present pattern of results and the pattern observed by Matin et al. (1969, 1970). These differences are more easily observed by representing the same data as in Figure 5. Figure 5 presents the same data as in Figure 4 but recalculated to reflect the position that the middle initial stimulus would

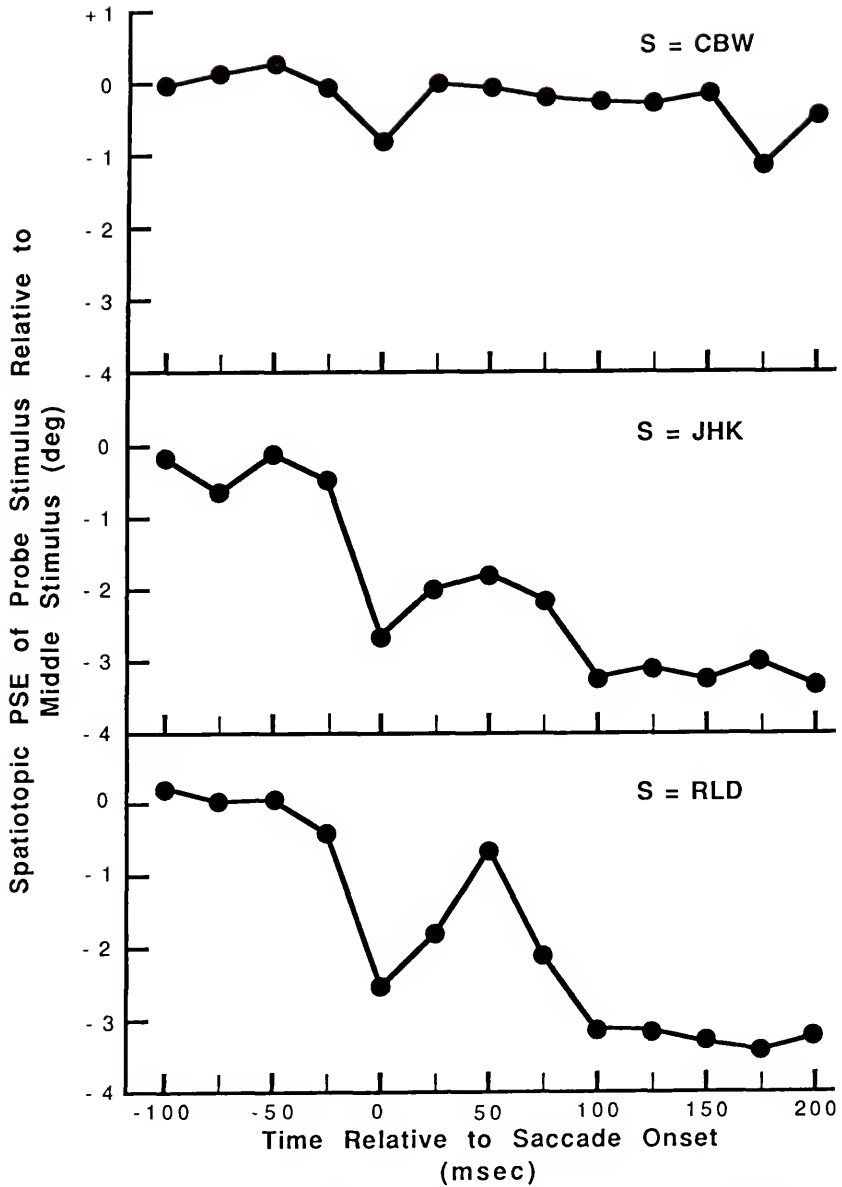


Figure 4. Point of subjective equality (PSE) between probe stimulus and middle initial stimulus. A PSE of 0 deg represents the actual spatial position of the middle initial stimulus. Left of the central initial stimulus is $< 0^\circ$.

have on the retina before, during and after the saccade (a retinal locus of 0 is the position of the fovea and negative positions are to the left). Thus, these data are in terms of retinotopic coordinates. The dashed line in Figure 5 represents the position on the retina that the middle initial stimulus would occupy if it had been present during the saccade. The present figure is analogous to Figure 10 in Matin (1972). Matin's (1972) data is different from the present data in two important respects: 1) He observed the changes in perceived direction beginning about 200 msec before saccade onset and lasting up to 300 msec thereafter. In the present data, the change in perceived direction is closely tied to the onset of the saccade, not being appreciably present until the 0 msec bin (which does contain some judgements up to 12.5 msec before the saccade begins). Moreover, the present data suggest perceived direction stabilizes by only 100 msec after saccade onset, not the 300 msec reported by Matin. 2) The data on the three subjects of Matin et al.'s (1969, 1970) are widely different in the accuracy, relative to the actual position of the initial fixation target in his experiments. No two of the subjects are at all similar in their judgements before or after the saccade. In the present experiment, a much greater degree of intersubject agreement was obtained. All three subjects were similar in their judgments before, during, and immediately after the saccade (Figure 4 and 5). After the saccade the three subjects diverged with two subjects overestimating the extent of the saccade while one accurately estimates the extent of the saccade (represented by judgements more negative than the position of the dashed line in Figure 5 after the saccade was finished).

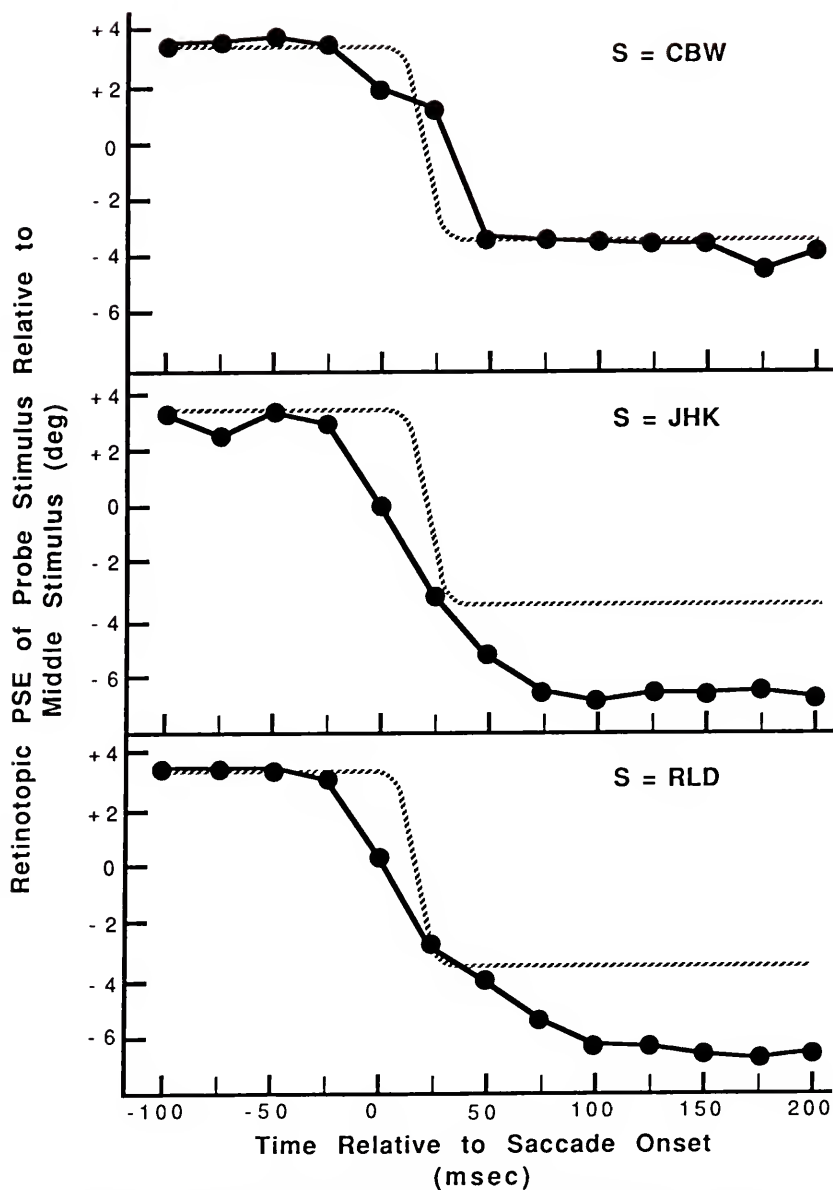


Figure 5. Corrected Point of subjective equality (PSE). Same data as in Figure 4 but replotted to indicate the position of the PSE on the retina. The fovea is set as a PSE of 0. The dashed line indicates the position on the retina where the middle initial stimulus would be imaged during a typical saccade, if present.

Still, the data are consistent with Matin's proposal that the data from the two-flash paradigm are affected by visible persistence. Despite the much closer proximity in time between the offset of the initial stimuli and the probe stimulus in the present experiment, there is no indication that judged direction maintains the same retinal locus until after the end of the saccade as in the above experiment (Matin, 1976a). Instead, the data follow closely the spatial position of the initial stimuli and, if anything, anticipate the eye movement to some degree.

The analyses to present have not allowed any assessment of Hershberger's hypothesis that perceived direction changes discretely and not in the continuous manner suggested by the above data presentation, especially in Figure 5. To test Hershberger's, proposal it is only necessary to look at the judgements made prior to or just after the saccade begins (-50 to 0 msec bins). Additionally, examining only the judgements from the two critical probe stimulus locations are important (1 and 2 in Figure 1). These probe stimulus locations are the only relevant locations because these are the only two probe stimulus locations for which judgements representing half the distance of the eye movement (3.4°) and the full distance of the eye movement (6.8°) are possible. Combining the data from these two stimulus locations and across subjects leads to the data presentation in Figure 6. If the stimulus at location 1 listed in Figure 1 is judged "far left", then that judgement falls into the 0° judged category. A judgement of "left" falls into the 3.4° category since the center of the "band" for judgements of "left" is 3.4° to the right of that probe stimulus location. Note that this band roughly represents a mislocalization of half the size of the eye movement. A judgement of "right" falls into the 6.8° bin for similar reasons. These

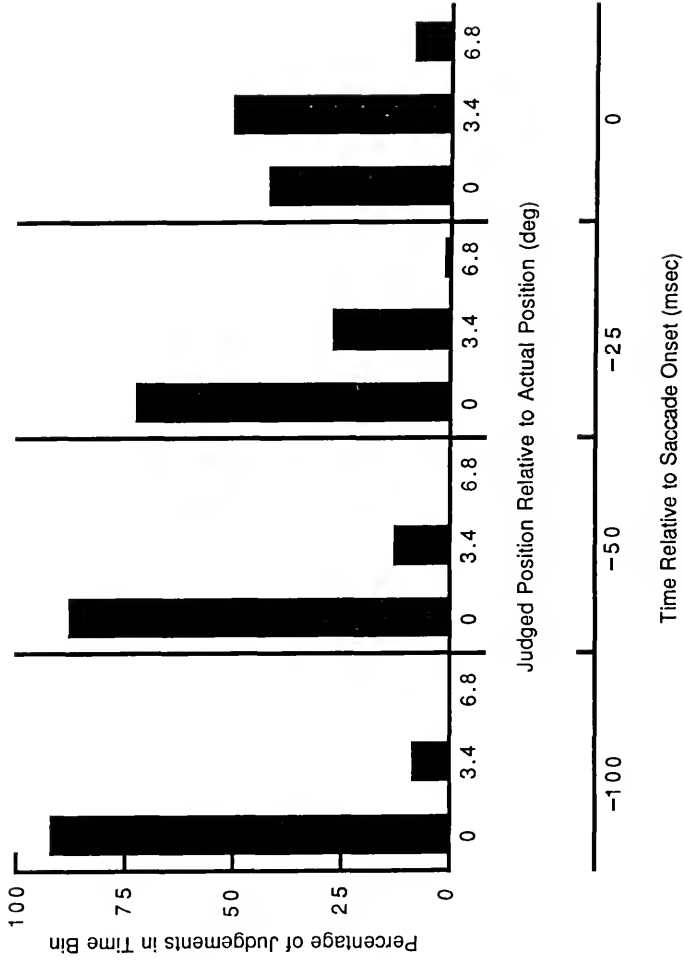


Figure 6. Percentage of judgements either correct, right approximately half the extent of the eye movement or right the entire extent of the eye movement at either 100, 50, 25 or 0 msec prior to saccade onset.

judgements of "right" represent mislocalizations of roughly the size of the intended saccade. For probe stimuli positioned at location 2, the judgements of "left", "right", and "far right" fall into the 0, 3.4, and 6.8° bins, respectively. The bins were then converted to percentages of the total number of judgements that fall into each time bin since the numbers were not equal.

If Hershberger's hypothesis regarding the afference copy were correct then Figure 6 should show progressively more judgements in the 6.8° position as the time bin is closer to saccade onset. Moreover, there should not be an increase in the judgements made in the 3.4° bin beyond that observed in the -100 msec bin which is shown as a comparison time period where judgements of direction were accurate (Figures 4 and 5). As can be seen, the predicted pattern does not hold at all, but instead judgements gradually become more concentrated in the 3.4° position until during the 0 msec time bin half of all judgements of direction fall in the 3.4° position bin, while only 9% of the judgements in this time bin fall the full 6.8° to the left. A chi-square test was performed on the data in the 3.4° position to test whether the increased judgements found in the 3.4° time bin represented a reliable increase. The proportion of judgements in the -100 msec time bin was used to determine the expected number of judgements for each of the other time bins as indicated in Table 1.

From these data, a chi-square was calculated for the three time bins (-50, -25 and 0 msec) on the possibility that the observed frequency at 3.4° differed from the expected frequency. The difference was significant ($X^2 = 190$, $df = 2$, $p < .025$). Given the fact that in the 0 msec bin contains judgements from trials where the eye has begun to move,

it could be argued that judgements could occur in the 3.4° . The basis of this argument lies in the fact that the actual eye position catches up with the perceived position of the eye under Hersherberger's proposal. Thus, a second chi-square test was performed using only the -50 and -25 msec time bins. This chi-square was also significant ($\chi^2 = 50.3$, $df = 1$, $p < .025$). Both tests indicate a large increase in the proportion of judgements of direction to be in the in-between position (3.4°), with few judgements ever reaching the position representing the full extent of the eye movement (6.8°). This test also indicates that perceived directions does begin to move in the direction of the eye movement prior to the onset of the saccade.

Table 1
Actual and Expected Frequency of Judgements of Varying
Direction Prior to Saccade Onset

Time Relative to Saccade Onset	<u>Frequency of Judged Position Relative to Actual Position (deg)</u>		
	<u>0</u>	<u>3.4</u>	<u>6.8</u>
<u>-100</u>			
Actual	89	8	0
(Percentage)	(91)	(8)	(0)
<u>-50</u>			
Actual	84	12	0
(Expected)	(88)	(8)	(0)
<u>-25</u>			
Actual	82	30	1
(Expected)	(104)	(9)	(0)
<u>0</u>			
Actual	29	35	9
(Expected)	(64)	(6)	(0)

Discussion

Basically, the results indicate that judged direction remains relatively closely aligned to actual direction with the deviation not becoming significant until about the time the eye movement begins. At that time, for all subjects the judged position becomes more accurate immediately after the end of the eye movement, while two subjects (JHK and RLD) show errors indicating that the eye was perceived to move farther than the actual extent of the saccade. Moreover, the results are not at all consistent with Hershberger's hypothesis that the afference copy controls psychophysical judgments of direction. The pattern of perceived mislocalizations prior to the beginning of the saccade are much more indicative of a gradual readjustment of perceived direction that does at least begin but does not finish prior to the onset of the saccade. This interpretation is supported by introspective reports made by all three subjects. All three reported on some trials perceiving the flash probe to move to the right. The motion was perceived to be continuous. Such a perception might be the result of the probe stimulus being perceptible for a period long enough prior to saccade that its perceived position was displaced while visible. Of course, the observations are only informal.

While the results are not strongly consistent with either Matin et al.'s (1969, 1970) data or Hershberger's hypothesis, the results do appear to replicate Bischof and Kramer (1968). They observed perceived mislocalizations prior to the onset of the saccade in the direction of the intended eye movement. Their data indicated a rapid readjustment of the perceived coordinate system just prior to the saccade in a manner

similar to what is observed here. The implications of the present experiment, along with that of Bischof and Kramer's (1968), is that the corollary discharge may be more able to be responsible for the shifts in perceived direction necessary for perceptual stability than indicated by Matin's (1972, 1976a) proposal of a slow corollary discharge. Yet, the corollary discharge seems to operate in a continuous manner more similar to an efference copy than Hershberger's proposed afference copy.

Still, how does one account for the slow change in perceived direction observed in Matin's (1972) display of the data of Matin et al. (1969, 1970). Hershberger (1976, 1987) placed a great deal of weight on the fact that the data were curvilinear in arguing that the data obtained by Matin et al. (1969, 1970) prior to the saccade was not due to memory factors. Hershberger, like Skavenski (1976), expected that memory factors should show a linear trend. Yet, if their expectation that the trend should be linear were in error, then in fact memory factors could explain the entire slow trend observed in the data of Matin et al. (1969, 1970) data.

The results of the present experiment raise some interesting questions. To best present these questions it is necessary to explore in more detail the observations made by Stevens et al. (1976) in a paralyzed eye experiment. Stevens et al. had been concerned that some of the perceptions of motion of the world made during attempted saccades when the eye was paralyzed actually resulted from small residual movements of the eye. To test this hypothesis, one of the subjects used by Stevens et al. was induced into extremely deep paralysis which did not allow any residual movements. In another procedure, the subject

was given a retrobulbar block which prevented eye movements while allowing movement of the remainder of the body. In both cases, the attempt to make a saccade was accompanied by a displacement of the perceived location of the world. Motion of the world was not perceived. These results were one of the observations that lead Hershberger (1987) to propose that the efference copy controlled readjustment of perceived location in a discrete manner. Given the results of the present experiment that perceived location is readjusted in a continuous manner, why is this motion not perceived, particularly in the experiment of Stevens et al. (1976)? One possible reason could be that there is sufficient suppression of the ability to perceive motion that during a saccade the smooth displacement of the world would not be perceived. The second experiment will explore this possibility.

CHAPTER III
EXPERIMENT 2:
SACCADIC SUPPRESSION OF MOTION DETECTION

There have only been a few attempts to measure the degree to which a subject's sensitivity to motion detection is reduced during saccadic eye movements. The general conclusion is that motion sensitivity is reduced somewhat, but not nearly to the extent necessary to obscure motion of the size created by the extent of the eye movement (Bridgeman, Hendry, & Stark, 1975; Heywood, 1981; Mack, 1970; Stark, Kong, Schwartz, Hendry, Bridgeman, 1976). The two most systematic studies find detection for motions larger than about 1/5th to 1/3rd the size of the saccadic eye movement (Bridgeman et al., 1975; Mack, 1970). Such a meager amount of suppression can not account for the apparent degree of motion suppression observed by Stevens et al. (1976) in their paralyzed eye experiment.

Careful analysis of the experimental situations used in the various experiments yield some possible explanations for the apparent discrepancies between the two sets of observations. In the studies reporting on motion detection, it is possible that the studies actually only measure sensitivity to displacement of a stimulus to a new location after the eye movement had ended. By displacement, it is meant that the subject perceives the stimulus is in a new location but does not perceive the actual translation of the stimulus, that is, the subject does not perceive the actual motion of the stimulus. Such a confound is possible because these experiments employ stimuli that are 1) asymmetrical, 2) nonrepeating, and 3) present before and after the end of the

saccade. These three elements allow the subject to perceive that a displacement had occurred in the stimulus without perceiving the stimulus traversing the positions in between the end points of the motion.

For example, Mack (1970) used a single dot on an oscilloscope that was moved during the eye movement in response to a signal derived from the EOG. Bridgeman et al. (1975) used a pattern of 13 fixation lights. The subjects were instructed to make saccades at will along these lights and it was these patterns of lights that were moved during the saccades, i.e., the target fixation light would move during the saccade. Moreover, the mechanical system used by Bridgeman et al. (1975) to make stimulus motions could be heard by the subjects. Bridgeman et al. admitted that the estimate of reduced motion sensitivity during eye movements was conservative.

Basically, these previous experiments suggest that motion sensitivity is reduced during eye movements. Despite the biases against finding such suppression, the results in all cases do display some reduction of sensitivity to motions over the condition where the eye is still. Yet, these experiments do not provide an adequate measure of the degree of motion suppression. To obtain a better estimate of the magnitude of motion suppression, at least two alternatives are possible. First, the entire stimulus configuration that is in motion could be only presented during the saccadic eye movement. With this procedure, no displacement would be present, but unless the stimulus is chosen very carefully, motion detection in this situation could become confounded with detection of luminance changes. The second alternative would be to use a stimulus that moved in a specific way so that the stimulus configuration was identical both before and after the end of the eye movement. Again, no displacement information would be present outside of detecting the motion. This alternative could be realized by presenting a

grating to the subject and moving that grating during the saccade across distances that are whole multiples of the spatial period (the inverse of the spatial frequency). If this motion is accompanied by removal of cycles at the edge towards which the motion occurs and addition of cycles at the other end of the stimulus, then the static stimulus will not change at all relative to the subject either before or after the saccade has occurred. Using this methodology, the degree that sensitivity to motion detection was reduced during saccadic eye movements was measured in the second experiment.

Method

Subjects

Four subjects (3 male, 1 female) were used, ages 20 to 30 years old. All subjects had normal acuity in the eye used in the study. One subject (JBM) was discovered to have a mild ablyopia in her left eye after she ran in the experiment.

Apparatus

The apparatus was the same as in Experiment 1.

Procedure

In this experiment the viewing distance was increased to 32". The electrode placement to record the EOG was identical to that used for the first experiment.

The procedure for the present experiment employed a two-alternative-forced-choice paradigm, with two types of trials, saccade and nonsaccade.

During saccade trials, an initial fixation bar will appear superimposed upon a 2 cycle/° horizontal square wave grating with a Michelson contrast of 16%. The duty cycle was 40% lighted. The subject was instructed to fixate on this target. After 1 second, this initial fixation target was extinguished and simultaneously a second fixation bar was presented 2° to the right. The second target was on for 180 msec, shorter than the normal latency for a saccadic eye movement. This sequence of events was then repeated with both periods being subject-initiated. Randomly, in either the first or the second time period, the grating moved 1, 2, 4, 8, 12, or 16 complete cycles (or 0.5, 1, 2, 4, 6, 8°). During the motions, the contrast of the grating reduced to 12%, still above the contrast threshold for still gratings during 2° saccadic eye movements (Volkman, Riggs, White, and Moore, 1978). The motion was triggered off the horizontal EOG so that the motion occurred during the early portion of the eye movement when suppression for motion, as well as detection, appears to be maximal (Bridgeman et al., 1975; Volkman, et al., 1968). The subject's task was to report whether the motion of the grating occurred during the first or second period. Both the EOG and the trigger derived from the EOG were monitored during both periods of the trial. The trial was rejected and repeated later if a false trigger occurred.

The nonsaccade trials were identical except that the second target never occurred. The motion of the grating occurred briefly after the end of the first target either during the first or second period. As in the saccade trials, the subject was to report during which period the motion occurred.

To better compare the present results with the results obtained by Bridgeman et al. (1975), the velocity was kept constant across all motion sizes. The velocity was 770°/second. Thus, the different motions sizes confound different motion extents with different durations.

Subjects were run in 4 sessions of 180 trials each (not including trials rejected). Within each session there were 6 blocks of trials (3 saccade and 3 nonsaccade). There were 120 saccade trials, 40/block, and 60 nonsaccade trials, 20/block. During a session, each motion size was presented 20 times during saccade trials and 10 times during nonsaccade trials. Half of the motions for each size and each trial type were to the left and half were to the right. Block type was alternated within each session with the type of block presented first during the first session randomized across subjects. After the first session, the block type presented first was alternated, that is, if a block of saccade trials was presented first during the first session, then a nonsaccade block of trials would be presented first during the second session, *et cetera*.

The responses were input into the Commodore microcomputer by the experimenter for offline analysis. Threshold of motion detection was calculated at the motion size detected on 75% of the trials, corresponding to a d' of 1 in signal detection methodology (Green & Swets, 1966). If no motion size was detected exactly 75% of the trials then a linear interpolation between the two motion sizes on either side of the 75% detection level was performed to estimate the motion size that would be detected 75% of the trials.

Results

Thresholds did not differ for motion to the right or to the left during nonsaccade trials. Consequently, the data were combined and will be reported together. Motion to the right during saccade trials will be referred to as "motion-with" since the stimulus motion is in the same direction as the eye

movement. Motion to the left will be referred to as "motion-against" as the stimulus motion is in the opposite direction of the eye movement.

Figure 7 plots the psychometric function for each subject relating the percentage of correct detections to the size of the stimulus motion. For all four subjects the psychometric functions for the nonsaccade functions have steeper (that is, larger) slope than those obtained from saccade trials. Without exception, detections were perfect for nonsaccade trial motions 4° and larger. Perfect detections were never observed for any motion size during saccade trials. Subject CBW approaches completely perfect detection during saccade trials, especially for motion-with trials where detection of greater than 90% correct were observed. The shallower slopes indicate that using a stricter criterion for calculating the threshold, for example 90%, would indicate a larger magnitude of suppression during saccades than reported in Table 2 below. Thus, the thresholds reported in Table 2 represent a conservative estimate of motion suppression. Two more features of note: 1) for the three subjects that reached threshold during saccade trials (GER, JHK, CBW) the slope of the motion-against trials up to at least threshold is lower than for motion-with trials, and 2) for all subjects, the percentage of correct detections for 6° motions during motion-with saccade trials are less than either 4° or 8° motions. In fact, for subjects JHK and GER, the percent correct detections during the 6° motions during motion-with saccade trials fall below the 75% threshold levels. The thresholds to be reported in Table 2 were calculated from the first motion size that reached the threshold criterion and, in essence, represent lower bounds for the estimates of the thresholds for subjects GER and JHK. A more stringent threshold would lead to an even larger estimated magnitude of suppression.

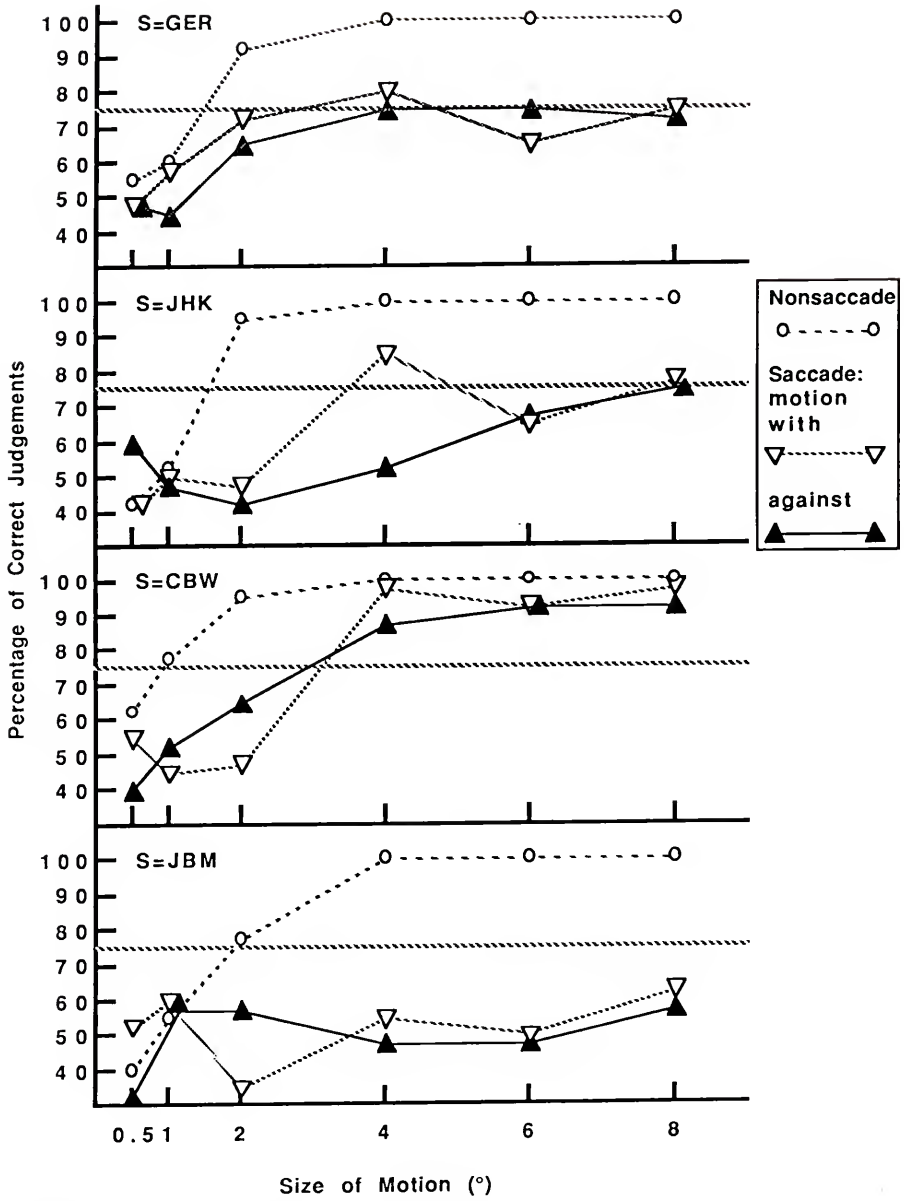


Figure 7. Percentage of correct detections of stimulus motion for each subject.

Table 2
Motion Detection Threshold During Saccade and
Nonsaccade Trials ($^{\circ}$)

Subject	Nonsaccade Trials	Saccade Trials:	
		<u>Motion-With^a</u>	<u>Motion-Against^a</u>
GER	1.4	2.7(1.9)	4.0(2.9)
JHK	1.5	3.6(2.4)	8.0(5.2)
CBW	0.9	3.1(3.4)	2.9(3.1)
JBM	1.9	--b	--b

^a Numbers in parentheses represent the ratio of the threshold during the saccade trials to observed for nonsaccade trials for the same subject.

^b This subject never reached to 75% correct detection level for even the largest extent of stimulus motion (8°).

As a summary, Table 2 shows the thresholds for motion detection calculated as described above. One subject, JBM, never reached the 75% correct detection level for motion in either direction during saccade trials, which is why there is not a figure reported for threshold. Also reported in Table 2 are the ratios of the thresholds obtained for saccade trials relative to the thresholds obtained during nonsaccade trials. This ratio represents one way of measuring the magnitude of suppression of motion detection. Inspection of Table 2 shows that motion needed to have been approximately 3 times the extent (or three times the duration, see below) in order to be detected during a saccade than when the eye is fixating. This ratio is very similar to the 0.5 log unit elevation typically observed for saccadic suppression studies measuring detection of luminance changes. Recall that this estimate of suppression may be conservative, especially for JHK and GER. It is also noteworthy that all of the thresholds in the present experiment indicate that a motion larger than the 2° eye movement is necessary to be perceived. Also,

for GER and JHK the saccade trial thresholds for motion-with (stimulus motion to the right) seem to be much smaller than thresholds for motion-against.

Discussion

The results of the present experiment clearly demonstrate that the ability to detect motion is reduced or suppressed during saccadic eye movements. The amount of suppression, if measured using the 75% threshold detection criterion, is about the same 0.5 log unit suppression typically found in saccadic suppression studies measuring thresholds for detection of changes in luminance. Importantly, at least under the stimulus conditions employed in the present experiment, a motion the size of the eye movement in either direction was not reliably detectable. Based on this result, it appears that suppression of motion detection could be sufficient to prevent the subject in Stevens' et al. (1976) study from perceiving movement during attempts to execute saccades.

One of the more unexpected results was the difference in the psychometric functions for motion-with versus motion-against saccade trials. The reasons for differences in the psychometric functions for motion-with versus motion-against trials are not immediately obvious. One possible reason is that the stimulation of the retina is not identical for motion-with versus motion-against. Each direction of motion differentially adds on top of the motion caused by the motion of the eye. As such, motion-against, being in the same direction as the motion caused by the eye, is additive, while motion-with is subtractive being motion in the opposite direction. Thus, motion-with reduces or even changes the direction of motion on the retina while it occurs.

To explore what possible effects these vector sums might have on the present data, the vector sums were calculated with the simplifying assumption that the eye's velocity is constant during a saccade. A typical 2° saccade takes 30 msec (Bahill et al., 1975), giving a velocity of $67^\circ/\text{sec}$. Since these are vector sums, the signs are important. For these calculations motion to the right will be given a positive sign. Thus, the eye movement creates a motion vector of $-67^\circ/\text{sec}$ on the retina. Recalling that the stimulus velocity is $770^\circ/\text{sec}$, the resulting retinal velocities are:

Motion-with (stimulus moves to the right)

$$1) \quad 770^\circ/\text{sec} - 67^\circ/\text{sec} = 703^\circ/\text{sec},$$

Motion-against (stimulus moves to the left)

$$2) \quad -770^\circ/\text{sec} - 67^\circ/\text{sec} = 837^\circ/\text{sec}.$$

The change in retinal velocity is less than 10% of the presented stimulus velocity of $770^\circ/\text{sec}$. Still, these changes in velocity might play a role in the differences in the detectability of motion-with versus motion-against stimulus conditions.

Several issues not explored by the present experiment should lead to caution in interpreting the present results. The first issue is the confound between motion extent and duration that exists in this and other studies of motions suppression (Bridgeman et al., 1975; Stark, 1976). In all of these cases, the velocity of the motion was kept the same for all sizes of motion, but this fact meant that as the motion size increased, so did the duration of the motion. Thus, the thresholds obtained might not indicate the size of the motion necessary for detection, but the duration of the motion necessary for detection. While in either case the results indicate suppression of the ability

to detect motion, the interpretation of the results could be much different. If the duration of motion is the only relevant factor in the results from the present experiment, then motion much shorter than the duration of the eye movement is detectable (~10 msec for an 8° motion as compared to ~30 msec for a 2° saccade, Bridgeman et al., 1975). Mack (1970) chose to confound extent and velocity in his study of motion suppression. In all cases, the duration of the motion was the same as the duration of the saccade, only the extent, and thus the velocity, was changed. Still, his results are very comparable to those of Bridgeman et al. (1975) and Stark et al. (1976). From this lone comparison study, it appears that it is motion extent and not duration or perhaps even velocity that is the more critical variable for motion suppression.

Still, the velocity of the motion may be a variable that can affect motion suppression. To obtain sufficiently large motions in the present experiment extremely high velocities (770°/sec) were used. Bridgeman et al. and Stark et al. used an even higher velocity (900°/sec). Even in Mack's study, the velocities used were much higher than typical velocities perceived during normal experience. Yet, whether only high velocity information is suppressed or all motion is suppressed, it is high velocity stimulation that occurs as a result of a large saccadic eye movement. Suppressing only high velocity motion would still effectively suppress the perception of motion of the world caused by executing a saccade.

Another unresolved factor is the time course of the observed motion suppression. The timing of motions during trials was selected to occur near the beginning of the saccade. This time period was chosen because the maximum suppression of detection thresholds tended to be observed near the onset in other studies of visual suppression (Volkman, 1986). If the time course of what might be termed motions suppression is similar to the time

course of the suppression of detection of luminance changes, then this observation might explain why on some trials in Experiment 1, motion was observed to occur for the probe stimulus. If the probe was presented either early enough or late enough, the suppression might not have been great enough to prevent it from being observed. The observed motion tended to be in the direction of the eye movement. Thus, the likelihood is that the stimulus had been presented prior the saccade since the adjustment of direction appears to begin before the eye movement (see Chapter II).

One other factor of potential importance that could affect the ability to detect motion which has not been investigated in the present study is the contrast of the grating. Specifically, it seems reasonable that higher contrast gratings would be easier to detect. While this does not affect the comparison between saccade and nonsaccade trials, the absolute thresholds should be taken as specific to the contrasts used and not general. Still, as mentioned in the opening chapter of the present paper, the high velocity of the eye motion leads to a smearing of the retinal image which reduces the effective contrast. So, perhaps, the low contrast gratings used here might effectively mimic real world saccadic motion stimulation.

Unfortunately, one stimulus condition could not be implemented on the present equipment and, as a result, a determination of the source of suppression is made ambiguous. Ideally, a second nonsaccade condition would have been employed to some degree clarify the interpretation of the mechanisms responsible for the observed suppression. In this condition, during both parts of the trial, the grating would move in a manner consistent with the motion on the retina generated by the saccade, simulating saccade trials retinal effects. During one of these motions, one of the above used motions would be superimposed and the subject would report during which

part of the trial the superimposed motion occurred. Thus, the retinal motions would be identical for this trial type and for the saccade trials. The reason that this condition could not be implemented on the present equipment was that a video monitor was used to display the stimuli. Because typical 2° saccades last longer than video frames (30 msec versus 16.67 msec) the blank interval between frames would disrupt the presentation of the simulated saccade motion, even with the cylinder lens.

Still, a discussion of the logic behind this trial type will help in understanding the possible mechanisms of motion suppression during saccades, and the small uncertainty which remains after the current study. With this trial type, if thresholds between the nonsaccade trials and the simulated saccade trials were identical, then any observed suppression could be said to have arisen from an extraretinal source, since the critical factor leading to the elevated threshold was executing the eye movement and not the retinal stimulation. If, however, the saccade trial thresholds and the simulated saccade trial thresholds were the same, then the suppression would be likely to arise from a retinal source as changing the retinal stimulation, and not making the saccade, lead to the elevated thresholds. As a result, the suppression observed for motion detection in the present experiment (or any other experiments to date) cannot be ascribed to either retinal or extraretinal sources. Some tentative conclusions about the mechanisms of motion suppression are offered based on other sources of information. The suppression observed for changes in luminance suggests that it is likely both retinal and extraretinal sources are involved. In addition, if the present suppression is the mechanism that accounts for the subject in Stevens et al. (1976) only observing displacement and not motion of the world when attempting to execute a saccade with paralyzed eyes, then these results argue

for at least some role for an extraretinal mechanism. The fact that displacement and not motion were observed with the retrobulbar block, which prevents feedback from the extraocular muscles as well, argues that a corollary discharge must be involved to some extent.

In summary, the magnitude of motion suppression in the present experiment seems adequate to explain why motion of the world is not observed during either normal saccades or during carefully controlled paralyzed eye experiments. The present results suggest that there may be some type of asymmetry in the characteristics of suppression associated with the direction of the motion during the eye movement. Also, the mechanisms involved in the suppression have not been clarified, although some role for a corollary discharge seems likely.

In the first two experiments, psychophysical methods have been employed. These methods require verbal responses. The third experiment will examine the issue of stability around the time of saccadic eye movements from the perspective of a different response system. The final experiment will use a motor response, specifically body sway.

CHAPTER IV
EXPERIMENT 3:
SACCADIC EFFECTS ON MOTION INFORMATION
FOR POSTURAL RESPONSES

The vast majority of research concerning saccadic effects on vision, including the two previous studies reported here, have used psychophysical techniques and required verbal responses. Verbal responses seem a natural choice to ascertain visual functioning because verbal reports appear to be so closely tied to our conscious perceptions. More importantly, these techniques have proven valuable in uncovering clinically useful information (e.g., as measures of acuity, Riggs, 1965), and in uncovering functional aspects of sensory physiology (e.g., color mixture data and the different classes of cones and color opponent cells, Boynton, 1979). Still, a growing body of literature, that falls generally under the heading of "the two visual systems" theory, suggests that other types of responses use visual information differently (Leibowitz & Post, 1980).

The "Two-Visual-Systems" Theory

The two-visual-systems theory proposes that there exists a functional, if not anatomical, division of "the visual system" into two different modes of processing (Held, 1968, Leibowitz & Post, 1980; Schneider, 1967, 1969; Trevarthen, 1968). In essence, the theory proposes that the visual system is

divided into two subsystems. One subsystem, referred to as the *focal* (Trevarthen, 1968) or cognitive (Bridgeman, Kirch, & Sperling, 1981) subsystem is proposed to be the system primarily tapped by psychophysical techniques. The focal subsystem is proposed to be responsible for pattern recognition and other tasks requiring fine discriminations. Information stimulating the retina on or near the fovea contributes most heavily to focal subsystem processing (Johnson, Leibowitz, Milladot, & Lamont, 1976; Leibowitz, Roedemer, & Dichgans, 1979; Trevarthen, 1968). Foveal stimulation is of primary importance in focal vision because of the high acuity of the fovea allowing fine discriminations and the poor acuity of the periphery not allowing fine discriminations.

In contrast, the other subsystem, the *ambient* (Trevarthen, 1968), localization (Leibowitz & Post, 1980; Leibowitz et al., 1979), or motor-oriented subsystem, does not require the high acuity of the fovea for its processing. Thus, visual information from all portions of the retina contributes to ambient visual processing about equally (Johnson et al., 1976; Leibowitz et al., 1979; Trevarthen, 1968). The ambient subsystem processes information concerning the location of objects in space and the orientation of the organism with respect to the environment (Held, 1968; Schneider, 1967; 1969; Trevarthen 1968).

Anatomically, the retinal projections to the lateral geniculate nucleus (LGN) of the thalamus, and from the LGN to the striate cortex (that is, the central visual system) subserves the focal subsystem. The projections from the retina to the superior colliculus of the midbrain are proposed to subserve the ambient subsystem (Schneider, 1967, 1969). Placing a lesion in the visual cortex of the golden hamster causes the animal to be unable to learn a pattern discrimination task, while its ability to perform orientation tasks

appear unimpaired. Lesioning the superior colliculus causes the hamster to be unable to learn orientation tasks. If an orientation response is not involved, then the hamster can learn pattern discriminations (Schneider, 1967; 1969). A similar dissociation has been observed in monkeys with the forebrain commissures (anterior telencephalic commissure and corpus callosum) cut (Trevvarthen, 1968).

Evidence supporting the two-visual-systems theory has also been gathered from human patients with brain damage to various areas of the visual system. Some of this evidence has fallen under the term "blind sight." In this case, if the lesion affects the central visual pathways then the patient reports being unable to see ("blind") in the affected portion of the visual field. This report is confirmed by normal perimetry, i.e., the affected area of the visual field is a scotoma. Examinations of the patient using stimulus motion or a motor response have revealed that, if the superior colliculus is spared, visual function is not completely absent from the scotoma. Visual functions still present include 1) significant tendencies to execute saccades in the direction of objects imaged in the scotoma (Poppel, Held, & Frost, 1973; Weiskrantz et al., 1974), and 2) the ability to accurately point to an object imaged in the scotoma given that the object is sufficiently large (Perenin & Jeannerod, 1975; Weiskrantz et al., 1974). These spared visual functions are consistent with the functional and anatomical distinctions proposed by the two-visual-systems theory.

Functional separations of the operation of the visual system consistent with the two-visual-systems theory have also been observed in normal adult humans. The visual acuity of the periphery does not seem to be affected by changes in the refractive error of the image over a large range (Johnson et al., 1976). This fact is in dramatic contrast with the effects of refractive

error on foveal vision where errors of less than 1 diopter (inverse of the focal distance in meters) are considered clinically relevant and requiring treatment. Apparently, the normal functioning of the periphery does not require a clear image, as does the fovea (Johnson et al., 1976). A similar dissociation between stimulus parameters affecting foveal vision and an orientation response has been observed with circularvection (CV) (Leibowitz et al., 1979). CV is the perception of circular self-motion by a person when the person is actually still. CV is induced by a stimulus pattern moving in a circular direction around the person. The direction of self-motion is opposite to the direction of the stimulus pattern, thus the direction of CV is consistent with the actual direction a person would move to create the motion of the stimulus pattern if it were still. CV is only minimally affected by the presence of refractive errors of over 16 diopters or by reductions of luminance to near threshold levels. Both the large refractive errors and the low luminances used Leibowitz et al. (1979) would greatly disturb the perceptions of fine detailed patterns. Given that the perception of fine details requires the fovea, and CV can be thought of as an illusion of the subject's orientation relative to the environment, these results are consistent with the distinction between focal and ambient visual processing in the two-visual-systems theory.

Thus, several lines of evidence, which have been briefly reviewed, support the two-visual-systems theory. One implication of this theory is that psychophysical studies of vision primarily tap focal vision and not ambient vision (Bridgeman et al., 1981). By implication then, psychophysical studies of saccadic effects on vision may not completely describe how visual functions change during saccadic eye movements. The next section will review previous studies supporting this proposition.

Saccadic Effect on the Ambient Subsystem: Previous Studies

Only two studies have examined what might be termed saccadic suppression of ambient vision. In both cases, the studies have used postural stability as the response (Krantz & White, in preparation; White, Leibowitz, & Post, 1980). The rationale for using postural stability as a response for the ambient subsystem rests on the observations that 1) vision contributes to postural stability (e.g., Dichgans & Brandt, 1978), 2) the primary information necessary for postural stability is information about the organisms orientation relative to the environment (White, et al., 1980), and 3) the retinal stimulation associated with a saccade would indicate that the person was losing balance if it occurred when a saccade was not occurring (Krantz & White, in preparation; White et al., 1980). In other words, informal observation indicates that, during saccades, some sort of suppression of an ambient visual function may be occurring as well as suppression of visual functions required in psychophysical tasks. Both experiments support this informal observation.

Both experiments mentioned above used similar designs to measure saccadic suppression of body sway. The primary comparison was between trials where subject made saccades across a still stimulus surround and trials where the stimulus surround moved in a saccade like manner while the subject fixated. The retinal stimulation was very similar in both conditions. The only difference being whether the motion was made by a saccade or motion in the environment. Both studies found that the conditions in which

the saccade-like image motions were produced by the stimulus surround caused more sway than trials with actual saccades (Krantz & White, in preparation; White et al., 1980). In fact, Krantz and White observed that saccades may have even led to less sway than the baseline condition during which both the stimulus surround and the subject's eyes were still. White et al. did not observe this trend.

These studies also suggest ways in which saccadic suppression of body sway is different from saccadic suppression observed in typical psychophysical studies. Recall that Brooks and Fuchs (1975) found that motion of the visual scene can elevate thresholds to about the same degree as saccadic eye movements when the eyes are kept still. This observation is important to metacontrast explanations of saccadic suppression (Matin, 1974). The condition used by Brooks and Fuchs (1974) when high velocity stimulus motion was presented to the fixating eye parallels the simulation of the image motion caused by saccades used by both Krantz and White (in preparation) and White et al. (1980). In fact, by simulating the image motion of a saccade, the stimulus parameter for eliciting metacontrast effects should be very similar in the saccade and in simulated saccade conditions. Yet, suppression of body sway is only observed in the actual saccade conditions. Actually, all peripheral conditions are similar, except for any shearing force on the retina, between the actual saccade conditions and the simulated saccade conditions in the postural stability studies, suggesting that only an extraretinal mechanism may be involved in saccadic suppression of body sway (Krantz & White, in preparation; White et al., 1980). This conclusion is distinct from that reached with psychophysical studies of saccadic suppression, which suggests that both retinal and extraretinal mechanisms are involved.

The distinction between saccadic suppression observed with psychophysical studies, perhaps tapping the focal subsystem, and the studies of saccadic suppression using postural stability was further strengthened by the relationship between the magnitude of saccadic suppression and the size of the eye movement. As mentioned in the Introduction (Chapter I), psychophysical measures of saccadic suppression indicate that the magnitude of suppression increases as the saccade size increases. Krantz and White (in preparation), however, observed that the magnitude of saccadic suppression of sway is actually greater for small saccades ($<4^\circ$) than for larger saccades (4° and larger), which is opposite the trend found in psychophysical studies. This trend further supports the notion that some sort of extraretinal mechanism must be responsible for saccadic suppression of body sway. Above, retinal shear was the only peripheral mechanism that was not ruled out by the simulated saccades conditions to account for the suppression of body sway. Yet, since accelerations increase with increasing saccade size, the magnitude of any shearing force should increase with larger saccades (Alpern, 1971; Bahill, Clark, & Stark, 1975; Carpenter, 1977). It would be expected from this fact that increasing saccade size should lead to more, not less, suppression as observed. In fact, this observation tends to rule out retinal shear as a factor in any type of saccadic suppression since it operates at the level of the retina before any divergence between focal and ambient subsystems would be possible.

Even more directly relevant to the topic of the present paper is the observation by White et al. (1980) that motion of the surround stimulus during the time of a saccade does not seem to be as effective as the same motion when the eye is still. Several weaknesses in this particular experiment by White et al. (1980) suggest that this conclusion is tentative. In

their study, White et al., did not measure eye movements at all, but simply made the stimulus motion occur approximately 200 msec after the subject was cued to make a saccade by the appearance of the target stimulus. While the 200 msec delay represents a typical delay time for the execution of a saccade (Alpern, 1971; Carpenter, 1977), there is no objective measurement to verify that the stimulus motion occurred during the eye movement. And if Krantz and White's (in preparation) observation that simply executing saccades reduces body sway relative to baseline, then this factor could account for the differences observed by White et al., as there were not any saccades in the comparison condition. One of the motivations for the present experiment is to replicate White et al.'s observation when triggering stimulus motion off the saccadic eye movement.

While both Krantz and White (in preparation) and White et al. (1980) suggest that visual information to the ambient subsystem is suppressed during saccades, other studies indicate that information in the ambient visual subsystem is preserved. Studies involved in the debate over whether saccades are retinotopically or spatiotopically programmed provide one source of evidence that at least some aspects of visual information are preserved in the ambient subsystem. This debate centers on whether saccades are executed towards the location of the image of the object on the retina relative to the fovea (retinotopic programming), or if the brain tries to execute the saccade in order to image the spatial location of the object on the fovea (spatiotopic programming). In other words, are saccades executed using spatiotopic or retinotopic coordinates as discussed in Chapter I. While in most situations both types of programming will produce identical results, it is possible to identify situations where this may not be the case. Hallett and Lightstone (1976a,b) attempted to address this controversy by presenting

saccadic targets during a saccade. Their hypothesis was that if saccades are retinotopically programmed then the second saccade should not be accurate but in error when referenced to the spatial location of the stimulus, as indicated by psychophysical studies finding errors in perception of direction (the first experiment can be included in this list). Yet, they observed that, although a few saccade targets were "ignored" the saccades were accurate and of "approximately normal latency" (Hallett & Lightstone, 1976b, p. 107). But they did note that latencies to targets presented during saccades did have slightly longer than normal latencies, such that the latency of the second saccade as measured from the end of the first saccade was actually of a more normal duration (Hallett & Lightstone, 1976a,b). Still, these findings indicate a preservation of localization information in contrast to the findings of both psychophysical studies and White et al. (1980). Again referring to Chapter 1, these studies indicate a preservation of spatiotopic information despite changes in retinotopic information.

Hansen and Skavenski (1985) found a similar preservation of localization information with yet a different motor response. In their case, they measured accuracy of a hammer strike at the location of a flashed target presented before, during, or after a saccade. They found that the accuracy of the hammer blows varied little around the time of a saccade occurrence. This result appears to agree well with the results of Hallett and Lightstone (1976a, b). Actually, the small variations in the position of the hammer blow accuracy near the saccade onset may not be terribly inconsistent with the results of Experiment 1 which found only small localization errors until after the saccade. If the conjecture that failure of memory of the position of the three initial targets is correct in explaining the errors of localization after the end of the saccade in Experiment 1, then the results may be even more

similar to Hansen and Skavenski's (1985) which does not seem to have the same memory demand.

Thus, some results suggest a suppression of localization responses during saccades (Krantz & White, in preparation; White et al., 1980) and others suggest a preservation of possibly similar responses (Hallett & Lightstone 1976a,b; Hansen & Skavenski, 1985). But these studies may address different aspects of visual functioning of saccadic effect on ambient vision, in a manner parallel to the division between the types of visual information in Experiments 1 and 2 of the present paper. While information about the spatial location of a stimulus pattern is essential to perceive motion, White et al.'s study of the effects of motion on body sway during saccades is formally similar to the present Experiment 2. On the other hand, the studies of Hallett and Lightstone (1976a,b) and Hansen and Skavenski (1985) are more formally similar to the present Experiment 1 which does not incorporate any motion in the stimulus. Moreover, in the latter studies, the temporal information, when present, indicates that possibly the response uses information about location obtained after the end of the eye movement. Hallett and Lightstone directly observed an increase in saccade latency, while Hansen and Skavenski have not measured latency at all leaving open the possibility that the movement is programmed from information after the eye movement is completed.

The present study is an attempt to better clarify the above discrepancy. The study will measure body sway as the response as in Krantz and White (in preparation) and White et al. (1980). The stimulus conditions will be similar to Experiment 2. Some trials will present motions of a grating stimulus during a saccade, and during other trials the same stimulus motions will be presented while subjects fixate. In addition, the sway responses that

follow either a saccade or a stimulus motion will be averaged as in Krantz and White. Thus any time locked component, like those observed by Krantz and White can be detected and measured. This analysis provides some ability to look at issues of localization of the stimulus. Krantz and White found response average movements of subjects to depend upon the direction of stimulus motion for lateral sway. The present study will be able to test whether sway responses to stimulus motions depend on the direction of the motion during a saccade.

The basic design of the experiment includes a baseline trial in which the subjects maintain fixation and no stimulus motion occurs. This trial type serves as a way of reducing intersubject variability by making every subject his/her own control. Other conditions are trials with subjects executing saccades without any stimulus motions, stimulus motions during fixations, and trials of subjects executing saccades which trigger the motion of the stimulus. In this experiment, the eye movement was chosen to be 3° since the spatial frequency of the stimulus was .33 cycles/ $^\circ$. Also stimulus motions were either 3° or 6° . Thus, as in Experiment 2, the stimulus patterns will be identical before and after the end of the eye movement and/or stimulus motion so only motion and not displacement information should be able to lead to sway. Moreover, motions the size of the eye movement are interesting since they match the extent of motion caused by the eye movement. Motions the extent of the eye movement were subthreshold in Experiment 2 during saccades but not during fixations, so the choice of 3° motions was made. The 6° motions was chosen because motions twice the size of the eye movement in Experiment 2 tended to be close to threshold even when the motions occurred during saccades.

Method

Subjects

Eighteen subjects (12 female and 6 male) participated in the present experiment as volunteers. The ages of the subjects ranged from 22 to 40 years of age. None of the subjects reported any previous history of postural problems, unusual dizziness, or diseases that affect any sensory organ associated with balance. Any prescription for corrective lenses was worn by subjects during the conducting of this experiment.

Apparatus

The apparatus to amplify and generate trigger pulses from the EOG was the same as the one used in both Experiments 1 and 2.

The apparatus to measure body sway and generate the stimuli utilized a position detection/stimulus presentation system that has been described in detail elsewhere (Krantz, 1985; and especially Shuman, in press). Only a brief description of the apparatus will be presented here.

The entire system is referred to as the position sensor system (PSS) which may be broken into four subsystems: data acquisition subsystem (DAS), data processing subsystem (DPS), stimulus control subsystem (SCS), and stimulus presentation subsystem (SPS) (Shuman, in press). The localization of head position in space is accomplished by the DAS online, while the DPS stores the data onto disks for offline analysis. The DAS performs the localization of the head with two acoustic click sources, attached to a light weight head gear which the subject wears, and 4 microphone detectors positioned above the subject's head. A microcomputer (Challenger C1P) sends

a signal to each click source in alternation to emit a brief sound pulse and simultaneously starts four timers, one associated with each microphone. When a microphone detects the click, it stops its associated timer. These timers have then recorded the propagation time of the click from the acoustic source to the microphone, and this information allows the determination of the position of the subject's head in space (Krantz, 1985). Although more degrees of freedom can be resolved, presently only lateral or left/right, and front/back translation movements and rotation of the head about the mid-sagittal axis relative to a plane parallel to the floor are resolved by the DPS.

The SCS consists of another Challenger C1P microcomputer connected to a galvanometer driven SPS through an A/D converter. The SPS displays a square-wave grating of 0.33 cycles/° subtending over 180° horizontally and 115° vertically in the form of a half cylinder in which the subject stands (Shuman, in press). The contrast of the grating was 46%. Fixation points were also controlled by the SCS and were rear projected on the same stimulus screen by a 12" black and white monitor with a visual angle of 16°. The DAS controlled the operation of the SCS, and also the presentation of all stimulus events, by signalling the beginning of a trial (Krantz, 1985). To present motion of the grating during saccade and record the samples during which a saccade or grating motion occurred required modification to the PSS configuration described by Shuman (in press) and Krantz (1985). These are as follows: The trigger pulse generated by the onset of a saccade was fed into the SCS microcomputer. On appropriate trials, this pulse signalled the SCS to generate a stimulus motion as described below. To record the sample when a saccade occurred (or on some trials when a grating motion occurred), the SCS toggled a communication line to the DAS which stored the number of the

most recently collected sample. When data collection was finished, the DAS sent the number of the samples during which saccades or grating motions occurred to the DPS for storage and offline analysis as described below.

Procedure

The EOG was recorded by electrodes placed bitemporally with a ground electrode placed on the left mastoid as in Experiments 1 and 2.

Procedures that were identical across trial type were: 1) Every subject filled out an informed consent which requested the subject to inform the experimenter of any history of problems with balance, unusual dizziness or problems with their inner ear. 2) The subject was positioned in the center of the half cylinder formed by the screen. 3) An initial fixation light was presented at the center of the screen for 500 msec at the beginning of the trial. 4) Subjects stood on one foot, and the same foot was raised just prior to each trial. When the subjects stabilized, the experimenter began each trial and placed himself in a position to assist the subjects in case they lost their balance. None did. 5) At the end of each trial, the subjects lowered the raised foot so that fatigue was minimized. And 6) the subjects had a break after half of the trials. There were four different trial types with different types of stimulus/cyc movement events. They were: baseline, saccades only, stimulus motion prior to saccades, and stimulus motion during saccades.

During the baseline trials, the stimulus surround stayed still and the subjects were instructed to keep their eyes positioned towards the location of the initial fixation point. In all other trials, 3° saccades were executed as signalled by the occurrence of fixation lights rear projected onto the screen. Saccades were executed in pairs. The beginning of a saccade pair was signalled by the presentation of a fixation light in the position of the initial

fixation light for 500 msec. About 50 msec after the initial fixation light was extinguished, a second fixation target was presented 3° to the right of the first target. The second target was on for about 150 msec, or shorter than the typical delay between target onset and saccade onset. Then no fixation target was presented for a random period of time of more than 1.2 seconds and not more than 2 seconds to allow a sufficient period of time for the averaging of sway responses (Krantz, 1985). Leftward saccades were then signalled by the next presentation of the first fixation light. In all trials, other than baseline trials, subjects executed 10 saccade pairs. The saccades to the right were the eye movements relevant for the presentation of motion and data analysis.

In the saccade-only trials, no stimulus motion occurred. In the motion-prior trials, the stimulus surround grating was moved either 3° or 6° during the interval between the extinguishing of the first fixation target and the presentation of the second target. Both motions were approximately ramp like and had a velocity of $200^\circ/\text{sec}$ so the 3° motions lasted 15 msec and 6° motions lasted 30 msec. A higher velocity more comparable to that used in Experiment 2 was preferred but was unobtainable because higher velocities caused instabilities in the SCS that lasted much longer than the intended motion. During a trial, only one motion size occurred, half (5) were to the right and half were to the left. In the motion-during trials, the occurrence of a stimulus-surround motion was triggered by the onset of a saccade to the right following the extinction of the second fixation stimulus. Again, depending on the trial, either 3° or 6° stimulus motions occurred. Typical 3° saccades last 30 msec (Bahill, et al., 1975).

Trials lasted 20 seconds with a sampling rate of 10 Hz. Only 10 stimulus motions occurred, 3° stimulus motions represent .75% of a trial and 6° motions 1.5% of a trial. The twenty saccades occupied only 3% of the trial

time. Since both 3° and 6° motions were used, there were six specific types of trials, with 4 replications of each trial type giving 24 total trials. The first twelve trials, consisting of two trials of each type were randomized across subjects, with the second 12 trials being the reverse of the first 12 for the same subject. The EOG and trigger signal were monitored on every trial to ensure that triggers were well aligned with the rightward saccades. Because an individual false trigger could not be prevented from affecting the data stream trials, the monitoring was for overall accuracy. On about 90% of all individual saccades the trigger was aligned accurately with the saccade occurrence.

Data Analysis

The samples of head position over time that are measured by the PSS can be thought of as a wave form. This wave form can be submitted to a fast-Fourier transform (FFT) which analyzes the wave form into the amplitude and phase relationships of sine wave components that would make up this wave form based on the assumption that the observed wave form represents one cycle of an infinite wave form. In the present experiment, only the powers, the square of the amplitude, were used for data analysis. The power at a frequency is the square of the amplitude at that frequency. For purposes of the present experiment, the resulting frequency components were subsequently grouped into frequency bins to give greater stability to the data. These frequency bins were then averaged within subjects across replications of trial types. Comparisons across conditions could be made by dividing the power at one frequency bin in one condition by the power at the same frequency bin of another condition. The resulting ratio gives the gain in sway for that frequency component of one condition relative to the

other. Taking the logarithm and multiplying by 10 converts the ratio to decibels (dB's) where an increase in sway for the condition in the numerator is given by a positive gain and a decrease is indicated by a negative gain.

Response averages could be calculated on trials with either saccades or stimulus motions because the sample where a motion or eye movement occurred was stored by the DPS. Offline the movement of the subjects were averaged both within and across subjects for the 2 seconds following the stimulus motion or eye movement. For the motion-prior trials, the averages were taken relative to the onset of the stimulus motion. For the motion-during, the averages were also taken from the onset of the stimulus motion, which also coincided with the onset of the eye movement as signalled by the EOG. In these two trials, averages were done separately for both left- and rightward stimulus motions. The saccade-only trials were averaged relative to the onset of the rightward saccades following the second fixation target.

Results

Observations of the EOG indicated that the subjects had no problem making eye movements according to the instructions. Baseline trials rarely had any eye movements, and during the other trial types saccades occurred as indicated by the fixation targets. Also important was the lack of any evidence indicating that the stimulus motions lead to any type of eye movement, reflexive or voluntary. At least, no eye movements reached the level discernible on the EOG of approximately 0.5° .

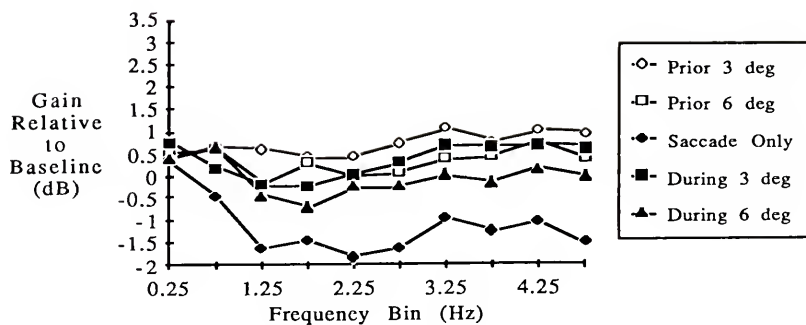
FFT Analysis

The typical power spectrum contains the majority of sway power in the frequency components below 1 Hz. As gain measures are relative measures, this general shape should be kept in mind. Also, it is relevant that stimulus events occupied only a small proportion of any trial.

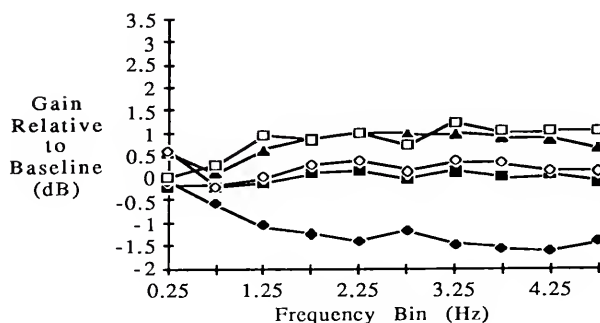
For all FFT analyses, the power spectra from individual subjects were grouped into 0.5 Hz bins with center frequencies from 0.25 Hz to 4.75 Hz. Then repetitions of the same trial type were averaged before the gains were calculated. After these gains were calculated within subject, then the gains were averaged across subjects.

In the first analyses, the gains of the five stimulus event conditions, saccade-only, 3° and 6° motion-prior, and 3° and 6° motion-during, relative to the baseline conditions of eyes still with no stimulus motion were calculated. The average gains across subjects are presented in Figure 8a, b, c. In all cases the gains were small as expected from the small amount of stimulus motion used to improve response averaging. No strong spectral signature was found for any condition, as is seen by the relatively flat and smooth profiles. Still some important trends in the data appear.

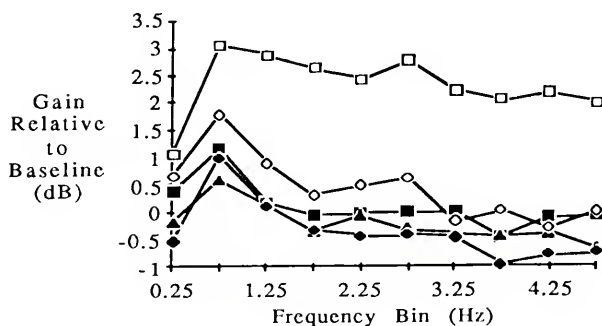
As found by Krantz and White (in preparation), the saccade only conditions uniquely tended to show negative gains across all three axes. This trend toward negative gains was significant using the binomial test, collapsing across all axes of sway measured ($p(27|30) = 3.7 \times 10^{-6}$). The n of 30 comes from collapsing across the 3 axes with 10 frequency bins each. The one difference in the stimulation between saccade-only and baseline trials was that during baseline trials the fixation lights did not flash on briefly, but remained off.



(a)



(b)

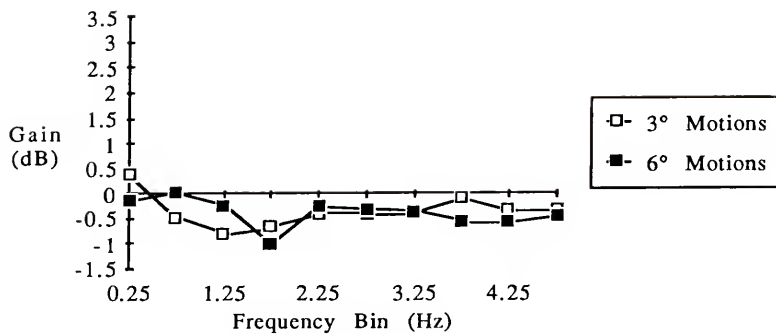


(c)

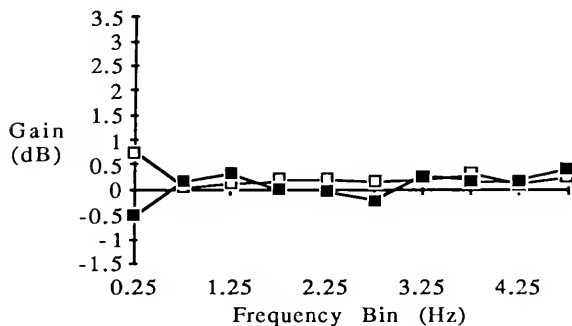
Figure 8. FFT gains for the various stimulus conditions listed in the legend relative to the baseline condition. a) Gains for the lateral sway axis. b) Gains for the fore/aft sway axis. c) Gains for the head rotation axis.

One of the most notable features evident from Figure 8b of the fore/aft axis is the fact that the gain appears to be closely related to the size of the stimulus-surround motion and not when the motion occurred relative to a saccadic eye movement. The smallest gain (actually negative) is with the saccade-only condition. Both 3° motion-prior and motion-during trials have very similar gain spectra with gains larger than saccade-only gains. The 6° motion conditions have the largest gains, irrespective of whether the motion occurs prior to or during the eye movement. This initial FFT analysis does not give a clear picture of whether there was any sway suppression or not because it does not directly compare the motion-prior and motion-during conditions.

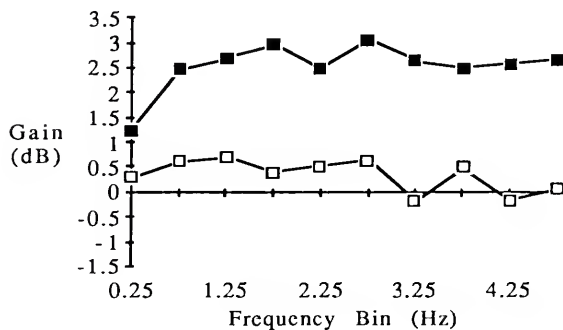
To get a better measure of any suppression of body sway in response to stimulus surround motions during saccades, gains were calculated for the 3° motion-prior trials over the 3° motion-during trials, and similarly for the 6° motion-prior over the 6° motion-during trials. These results are presented in Figure 9. Figure 9a,b presents lateral and fore/aft sway respectively. These sway axes do not show any evidence for sway suppression. All of the gains are near 0 dB. The finding for fore/aft sway was clearly anticipated by the gains relative to baseline shown in Figure 8b, where the size of the gain depended more on motion size and not when that motion occurred. Yet, the head rotation axis does show evidence of sway suppression for both 3° and 6° motion sizes. The gains tend to be positive, with the 6° gains tending to be quite large given the small proportion of the trial during which motion occurred.



(a)



(b)



(c)

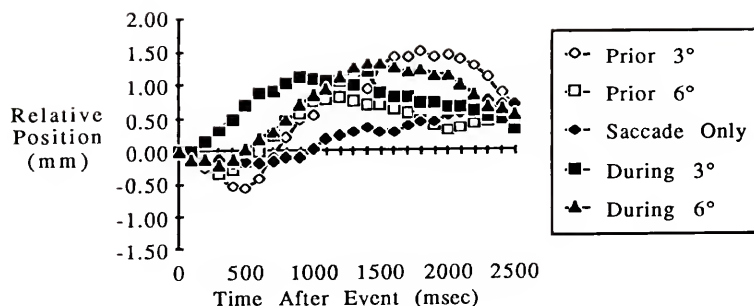
Figure 9. FFT gains for motion-prior conditions relative to motion-during conditions. a) Gains for the lateral sway axis. b) Gains for the fore/aft sway axis. c) Gains for the head rotation axis.

Response Average Analysis

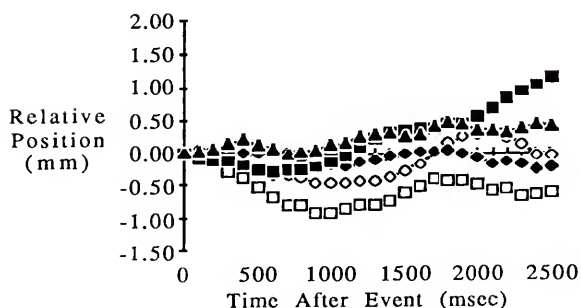
In addition to the gain analysis, the data were submitted to an response average analysis. This analysis was accomplished by averaging the sway position of the subject relative to the position of the subject at the onset of a same motion (in the same direction).

The averaging was done across repetitions of the trial type and subjects, as well as within motion size (3° or 6°), trial type (saccade-only, motion-prior, and motion-during) and the same motion direction (left vs. right). Figures 10 and 11 display these response averages for left and right motions, respectively. The saccade-only average responses are repeated on both left and right motions even though averaging was only done for the rightward-going saccades.

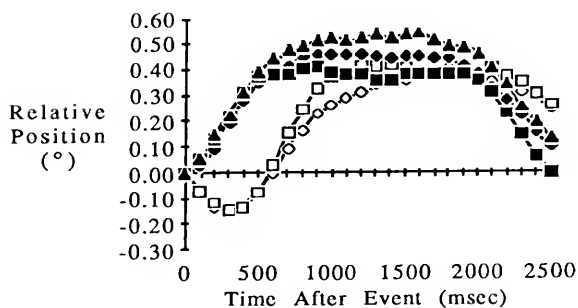
The rotation average movements are the clearest (Figures 10c and 11c). For both left and rightward stimulus motions, the 3° and 6° motion-during trials show average movements that are very nearly identical to the average movements for the saccade-only trials. There are slight but highly reliable motions in the direction of the eye movement (the standard errors of the peaks are in excess of 10 z units), this motion is similar to the motions observed by Krantz and White (in preparation) for head rotations during saccade only trials. The motion-during response average movements are distinctly different from the response averages obtained for the motion-prior trials. In this case, regardless of the direction of the stimulus motion, the subject rotated slightly to the left first and then to the right. The observation that the motion-during response averages are much more similar to the saccade-only response average movements than to the motion-prior response average movements suggests that the sway response "evoked"



(a)



(b)



(c)

Figure 10. Response average movements following the onset of either a saccade (Saccade-Only) or rightward stimulus motion (all other conditions). a) Response average movements for the lateral sway axis. b) Response average movements for the fore/aft sway axis. c) Response average movements for head rotation.

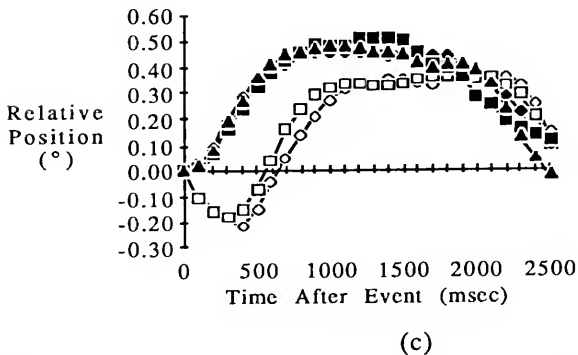
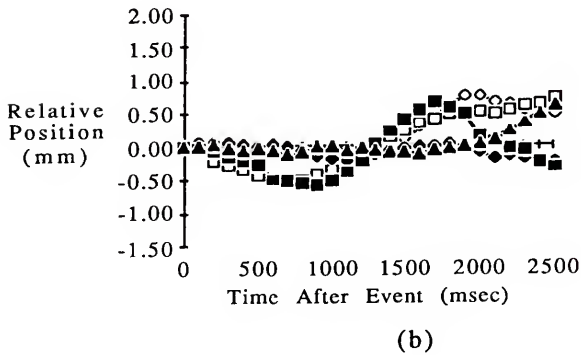
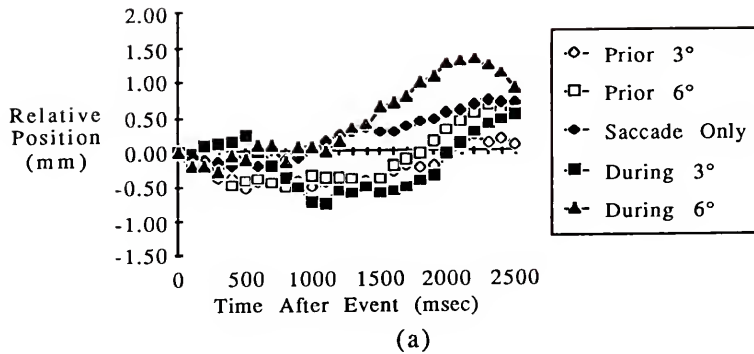


Figure 11. Response average movements following the onset of either a saccade (Saccade-Only) or leftward stimulus motion (all other conditions). a) Response average movements for the lateral sway axis. b) Response average movements for the fore/aft sway axis. c) Response average movements for head rotation.

by the stimulus-surround motion was "suppressed" during the saccade for both the 3° and 6° motion sizes.

It might also be noted that the response average movements for the head rotations do not return to 0 or the starting location. It might be possible that the head is simply making slow rotations to the right. Examination of the sway averaged across the entire trial across all subjects reveals that this is not so. The variability is quite large in the later periods of the response averages. The fact that the response averages do not return to the starting location is an artifact.

While the results are not as clear for the other sway axes, they are generally similar. On the lateral axis, motion-prior trials show an initial leftward movement. If the motion is to the right, the leftward movement is followed by a rightward motion that is absent if the motion is to the left. The pattern is rather unclear for fore/aft sway to rightward motions, but for leftward motions the motion-prior trials show a trend towards moving slightly towards the back of the subject that is absent during the motion-during trials. The response average movements are more strongly suggestive of suppression than are the gain analyses.

Discussion

The present data present a somewhat contradictory picture. Looking at the head rotation data, both from the FFT analysis and response average movements, it appears that motion information is suppressed in the ambient subsystem. A similar conclusion is tentatively reached from the response average movements for the fore/aft and lateral axes. It is not possible from

the present data to know if suppression differed between 3° and 6° stimulus surround motions. Yet, this conclusion is tempered by the observation, taken primarily from the FFT lateral and fore/aft data, that sway depends on the size of the stimulus surround motion and not when the motion occurred relative to the execution of a saccade (Figures 8b, and 9a,b). Perhaps some motion information is processed by the ambient subsystem, but not sufficient information to lead to a time-locked response average movement.

Relevant to the main thrust of this investigation, the present experiment suggests that suppression in the ambient subsystem for motion may be somewhat similar to suppression of motion information in the focal subsystem. In both experiments, motions the size of the eye movements were suppressed. One of the questions about the generality of the second experiment may have been somewhat answered by this third experiment. The equipment used in Experiment 2 required low contrast (12% during the motion) gratings to be used. In the present experiment, considerably higher contrast was achieved (46%). Yet, the suppression observed in the present experiment was still substantial, lending support to the contention that, because of the smear of the retinal image during a saccade, contrast of the grating may not be a very important factor.

Still, the suppression of motion information during saccades may not be quite as complete for the ambient subsystem. Suppression was not strongly indicated for either motions size for either the lateral or fore/aft axis on the gain measures. It is interesting that the evidence for motion suppression is clearly indicated by the head rotation axis. Perhaps why this axis was so suggestive of suppression is related to the relative masses of the head compared to the entire body. Given the small amount of stimulus motion during a trial, perhaps there was not enough stimulus motion to cause the

entire body to move sufficiently to achieve a clear picture of suppression. Despite this hypothesis, some motion information does seem to be processed by the ambient subsystem during saccades as most clearly indicated by the FFT data for the fore/aft sway axis (Figure 8b).

These results also show some interesting relationships to those of Krantz and White (in preparation). First, the tendency for the saccade-only trials to show less sway than the baseline trials is replicated. This might be related in some fashion to the fact that not making saccades for more than about a second (Bahill, Clark, & Stark, 1974) is an unnatural situation and the concentration on this task could in some way lead to slightly more sway. The tendency for saccades to lead to small head rotations in the same direction, as seen in saccade only trials, is also replicated. One of the interesting differences between the present results and the results of Krantz and White (in preparation) is seen in the average movements in response motions presented to the fixating eye. In the present experiment, there is not a relationship between motion direction and the direction of the average movement that was observed in Krantz and White. In the present experiment, the motions always start to the left for stimulus motions in either direction, for both lateral and rotation axes. In fact, the only indication of directional sensitivity in body sway responses is that motions to the left cause a longer lasting lateral leftward sway than motions to the right in the motion-prior condition. In Krantz and White (in preparation) motion-only trials were used without eye saccades during the experiment. Thus, the response averages may be altered by the need to execute another saccade, always to the right, shortly following the stimulus surround motion.

The fact that movement averages for fore/aft sway were not revealing is also similar to what was found by Krantz and White. In both cases, motion

for fore/aft sway is signalled in both directions (fore and aft) for motions in either direction (right or left). Thus, by and large, the present experiment, where consistent, replicates Krantz and White (in preparation), extending the notion that sway suppression includes motion during saccades and not just still surrounds.

In summary, motion information in the ambient subsystem is suppressed as it is for the focal subsystem. Some motion information does seem to be preserved but it does not seem to be responded to in the same way as equivalent motion during fixations. These basic findings seem at odds with the findings by Hallett and Lightstone for saccades to stimuli flashed during a prior saccade and by Hansen and Skavenski for abilities to strike objects flashed during saccades. Yet, Hansen and Skavenski report small but systematic errors to their targets during saccades. As a result, given the small size of the responses in the present experiments, the two studies may not be terribly inconsistent. Hallett and Lightstone do not give adequate results to see if they could be interpreted in a consistent fashion. Still, some motion information, including direction, is suppressed in the ambient subsystem. As with Experiment 2, it is impossible to separate peripheral from central mechanisms using the present results alone, but Krantz and White (in preparation) found that only an extraretinal mechanism could account for their results in the ambient subsystem. Since the same system is used in both studies it seems logical to assume that extraretinal mechanisms are responsible, primarily, for the results of the present experiment. The next and final chapter will examine all of the present experiments in the context of the question posed in the Introduction: Why does the world appear to remain stable during saccades?

CHAPTER V GENERAL DISCUSSION

Summary

The three experiments reported here took a divergent attack on the basic problem of why the world does not appear to move around the time of a saccadic eye movement.

The first experiment explored directly what happens to the perceived direction of an object around a saccade. The experiment was designed to determine whether perceived direction shifted in a continuous manner suggested by Matin's research (e.g. 1972, 1976a,b) or whether the shift was discontinuous as proposed by Hershberger (1987). The results clearly supported a continuous shift of perceived direction, but the shift did not appear at all like the trend observed by Matin. Matin observed that perceived direction shifted slowly when it was inferred that only a corollary discharge could cause the shift. Instead, the present study found a shift in perceived direction that is rapid and only just precedes the eye movement. The differences between the two patterns of results seem likely to be due to memory factors. In Experiment 1, significant errors in perceived direction were not observed in the data until after the eye movement was completed. These errors are, also, likely to be due to memory factors. This interpretation is strengthened because the judgements of direction were accurate and

consistent until after the change in eye position could act to perhaps disrupt the remembered location of the reference stimuli. In other words, until sufficient time and/or disruption by moving the eye occurred, judgements of direction were quite accurate. In Matin's (1972, 1976) studies all judgements of perceived direction were made at least a half a second after the offset of the reference stimulus. This time period is much longer than the time between reference and probe stimuli in Experiment 1.

The second experiment was designed to test if one reason the motion caused by the shift in perceived direction found in Experiment 1 is not normally observed was as a result of reduced sensitivity to motion during saccadic eye movements. To get the best possible estimate of any motion suppression, a grating was used as the moving stimulus. This grating was moved in such a way so that the pattern seen by the eye before and after the saccade was identical. In this study, suppression by a factor of about 3 was noticed and thresholds for motion detection were larger than the 2° eye movement used. It would be nice to interpret the results in terms of suppression relative to the size of the eye movement, but the low contrast and single size of eye movement used makes this interpretation untenable with the present results.

The third experiment shifts response systems. This experiment measured motion sensitivity during eye movements with body sway, a response controlled by the ambient visual system (Trevarthen, 1968). The pattern of results were complex but basically supportive of the interpretation that motion during eye movements does not affect body sway as much as motion during a fixation, and even when a response occurs, this response is different from the response to the same motion during a fixating eye. These results were similar to the results found for Experiment 2 using

psychophysical responses. This similarity occurred despite larger eye movements and much higher contrast used in Experiment 3 than in Experiment 2. Possibly Experiment 3 serves as an indirect extension of the generality of the results of Experiment 2.

In light of these results, the next section will describe in general terms how perceptual stability might be maintained. Next, the mechanisms that may be involved will be discussed.

Perceptual Stability: Description

A good way to discuss perceptual stability is in terms of the theory of Local Signs (Hering, 1879; Lotze, 1889). This theory attempts to account for how the brain interprets the direction of an object. In essence, the theory states that each part of the retina is associated with a particular direction. For example, an object will be associated with a direction 10° above the direction of gaze because its image falls on the retina a specific distance below the fovea determined by the optics of the eye. Thus, any stimulation of that receptor and associated neural architecture directly encodes some information about direction. In terms of retinotopic versus spatiotopic coordinates, each retinotopic coordinate is directly associated with a spatiotopic coordinate. The problem with this simple idea is that before and after a saccade, the same place in the world stimulates a different position on the retina, that is, the relationship between a particular retinotopic coordinate and spatiotopic coordinate changes as the eye moves. Yet, the brain somehow recalculates the local signs in such a way that directions relative to the body remain the same but the eye is given a new reference direction, perhaps associated with the

fovea. This recalculation or recalibration of the reference direction is so accurate that no part of the perceived world appears to move. This recalibration can be thought of as establishing the new and correct relationship between retinotopic and spatiotopic coordinates.

The results of the present experiments suggest that this recalibration of the local signs begins just prior to the eye movement and concludes before the eye movement is finished. This interpretation explains the present results, including the informal reports of motion in the direction of the eye movement. It also explains Hershberger's observation that saccading towards a low level flickering light causes a pattern of flashes to be imaged on the retina towards the eye (an observation replicated by the current author). This observation, present with every attempt and supporting the results of Experiment 1, suggests that the recalibration must be finished prior to the end of the saccade.

Yet, this recalibration usually goes unnoticed despite the potential to cause apparent motion of the world. The research typically associated with the term saccadic suppression suggests one reason the apparent motion is unnoticed: visual sensitivity is reduced by about a factor of 3 (Matin, 1974; Volkman, 1976, 1986). Above this general reduction in visual sensitivity, motion sensitivity is further reduced by about a factor of three and perhaps to such an extent that motions of the size of the eye movement are not typically noticed (Experiment 2). Suppression of motion does vary according to the size of the eye movement as observed by Bridgeman, et al. (1975) and Mack (1970), as does suppression of detection of an increment (Volkman et al., 1981). Thus, suppression appears to be adjusted to match in some way the perceptual disturbance that will accompany saccades of specific sizes.

Perceptual stability during saccades is not only important to our conscious perceptions, but perhaps even more to visual control over postural stability. It is also likely that the type of visual information is different for ambient versus focal vision. Suppression in the ambient visual subsystem (that portion of the visual system that provides information for postural stability) has been demonstrated to exist in a growing body of studies (Experiment 3; Krantz & White, in preparation; White, et al., 1980). The studies indicate that saccades do not create as much sway as would be expected from comparable visual motion. In fact, it seems as if making saccades leads to slightly greater stability than artificially holding fixation (Experiment 3, Krantz & White, in preparation). Moreover, the calibration of suppression for the size of the saccade does not seem to be present. Larger saccades are not associated with as much sway suppression as are smaller saccades. But, as in the psychophysical domain, motion during an eye movement appears to be suppressed. Motion during saccades both has less of an impact on sway, and when it does appear to affect stability the effects are different from those produced by the same motion to the fixating eye. First, there does not appear to be an effect of the direction of the motion on sway during the saccading eye. Second, even if the FFT spectra are similar for motions presented to the saccading and the fixating eye, the response average movements appear to be different (Experiment 3). Thus, suppression in support of perceptual stability exists in both visual subsystems, but suppression seems to operate differently in each.

Perceptual Stability: Mechanisms

In the Introduction, the mechanisms of saccadic suppression were broken down into two basic classes: retinal and extraretinal. The results of the present experiments lead to some tentative suggestions as to which of these mechanisms could be responsible for perceptual stability.

The shift in perceived direction (or recalibration of local signs) observed in Experiment 1 seems to have been the result of some type of extraretinal mechanism. The lack of visible cues to direction in the visual stimulation limits the role of a visible context as seen in Matin et al. (1969). While such mechanisms probably are important, the manner in which context may be used to enhance stability is still not well defined, though some type of matching of objects before and after the saccade seems implicit in these proposals.

Of the extraretinal mechanisms responsible for the changes in perceived direction, the present results suggest a centrally originating corollary discharge. Feedback theories and Matin's Hybrid theory are not strongly supported because the change in perceived direction clearly began prior to the onset of the eye movement. This fact does not rule out some role for feedback in portions of the readjustment of perceived direction that occur after the eye movement begins. The fact that the adjustment of perceived direction occurs before the onset of the eye movement suggests that the role of feedback is secondary and/or, perhaps, it acts as a fine adjustment (Steinbach, 1987). Moreover, it appears that feedback may be a slowly operating signal, too slow to be effective in perceptual stability around saccades (Steinbach, 1987).

While the mechanisms for the recalibration of local signs seems to be clearly extraretinal, and even of the corollary discharge type, the mechanism responsible for the suppression of the motion caused by the recalibration is not as clear. Again a corollary discharge probably plays a role in this suppression as found in the Stevens et al. (1976) study. The critical condition occurs when the eye is paralyzed and feedback is blocked in the retrobulbar block conditions. As mentioned earlier, displacement, or recalibration, of direction occurs when saccades are attempted, but no motion is observed. This condition eliminates retinal mechanisms as no stimulation to invoke these mechanisms was present and no feedback could have occurred by the nature of the block. Yet, it seems unlikely that other mechanisms are not involved in maintaining perceptual stability around the occurrence of saccades. Smear and masking are likely candidates to support any central mechanism, at least in helping to reduce motion sensitivity. Matin (1976b; Matin et al., 1982) has also found some evidence for visual context possibly playing some role in perceptual stability.

Again in the ambient visual subsystem, mechanisms for suppressing motion information cannot be clearly distinguished. Krantz and White (in preparation) and White et al. (1980) found that the corollary discharge was the best candidate to account for the reason that motion on the retina caused by a saccade was suppressed. The same motion without a saccade caused an increase in sway. The retinal stimulation, which was very similar in the two conditions, did not lead to the same outcome. Thus, mechanisms of suppression that depend upon the pattern of retinal stimulation alone do not lead to sway suppression. Yet, the same conclusion cannot be reached from the present experiment about suppression of motion stimulation (Experiment 3) which occurs during saccades. The necessary control conditions to determine this

were not used in the present experiment. Still, since the other relevant cases all point to a role for a corollary discharge, it seems likely that a corollary discharge plays a role in the present situation as well. This is especially likely as a corollary discharge is probably responsible for basic sway suppression.

The Central Role of the Corollary Discharge

Through all of the types of suppression discussed in this paper, including basic saccadic suppression, readjustment of perceived direction, motion suppression, and even suppression during blinks and vergence eye movements, the one mechanism that seems most universally present is the corollary discharge. It seems as if manipulating this signal causes the most change in perceptual stability. Going back to the original observations of the eye press and paralyzed eye, the corollary discharge appears to be the most universal mechanism. Volkmann (1976) came to a related conclusion when she proposed that the corollary discharge serves a function in saccadic suppression because it can operate in any visual environment, whereas others, particularly smear and metacontrast, can be limited by some visual environments. Moreover, the signal from the corollary discharge seems to convey the most information. It contains information about the occurrence of a saccade in advance of the eye movement beginning. This information can be used to modify visual sensitivity to a wide range of visual functions to prevent the effects of the saccade from being noticed. The corollary discharge is involved in the explanation of the first of the two basic questions about why saccades are not easily noticed. In the original theory of the corollary discharge, it also conveys information about the direction and extent of the

saccade (Sperry, 1950). Using a corollary discharge, recalibration of the local signs, if you will, can be begun before the eye movement begins. Functioning in this manner, the corollary discharge may be one mechanism involved in answering the question about why the world appears stable despite saccades.

The retinal mechanisms are not as able to indicate direction and extent, except for the ambiguous role of "visual context." They seem less likely to account for stability (Question 2) and are more involved in suppression (Question 1). Feedback could play a role similar to corollary discharge but it is unable to anticipate the occurrence of a saccade. Steinbach (1987) also proposes that the signal is a slow signal unable to respond to a disturbance of the type caused by a saccade. The corollary discharge seems to be best suited to playing a central role in making the visual effects of saccades goes unnoticed, principally because it can play a role in all facets of suppressing the perceptual effects of saccades under all visual situations.

Perceptual Stability: Plasticity

Before proceeding to the conclusions, one issue, alluded to in the Introduction and earlier in this chapter, needs to be addressed: Plasticity. Visual motor integration is not fixed. Early demonstration of the possibility of visuomotor integration can be found in inverting prism studies (Stratton, 1896, 1897). More relevant to the present discussion, the relationship between the signal to the eye muscles and the resulting eye movement changes during growth, and more dramatically after an operation to correct a strabismus (Steinbach, 1987). Since this motor signal does not bear the same relationship

to the perceptual effect of the eye movement, the resulting corollary discharge will not prove to be an effective signal for perceptual stability.

As a result, the system needs to be plastic (Held, 1961, 1968), with the corollary discharge being recalibrated as a result of changes in the relationship between the size of the motor signal and the perceptual result. It is in this role that feedback (Steinbach, 1987), and perhaps even the visual context (Matin et al., 1982), may play a role.

Unresolved Issues and Conclusions

Several issues still remain to be resolved. The most perplexing are how visual context might affect perceived direction as found by Matin et al. (1969) using saccades and Matin et al. (1982) with paralyzed eye experiments. Moreover, how do these mechanisms relate to the complex situation referred to as pursuit underregistration (Sullivan, 1987)? Basically, the pursuit underregistration phenomenon reveals inadequacies of perceptual stability while with saccades the adequacies of perceptual stability are stressed.

The fundamental question is that even though perceptual stability is understood in a qualitative way in the realm of saccadic eye movements, little is understood about how to integrate this situation with the rest of behavior. Included are how other types of eye movements, head movements, body movements, and even locomotion are all integrated into an overall perceptual stability. In each case, the local signs must be recalibrated to reflect the movement of the person. Of interest to the current situation, is that the theory of the corollary discharge was not developed to account for stability around saccades but for visuomotor stability in the face of body movements (Held,

1961; Holst, 1954; Sperry, 1950). While differences undoubtedly exist in the way perceptual stability is achieved in the face of different motor acts, the central role of the corollary discharge plays in reducing all the various possible effects of saccadic eye movements is suggested. Perhaps the corollary discharge may prove to be an integrating mechanism for general perceptual stability.

APPENDIX A CIRCUIT DIAGRAM OF EOG AMPLIFIER/TRIGGER APPARATUS

The amplifier portion of this circuit borrows heavily from the front end amplifier designed by Shuman (in press) for the microphone circuit in the PSS system. The rest of the circuit is almost identical to the trigger circuit designed by Dr. Robert Moore of Brown University. He provided me with his diagrams of his circuit that was used as the foundation for the present trigger circuit.

The circuit is built around one single operational amplifier (op amp) chip (a LM725) and 2 four op amp chips (TL074)(Figure A-1). Input power lines are ± 12 V, +5 V and ground. The LM725 provides a front end amplification of 60 dB with adjustable offset. The first TL074 provides further amplification adjustable from 5 to 10 dB, and filters the eye movement signal into a wave form proportional to the instantaneous velocity of the eye movement. This filtering (centered on 100 Hz with a 3 dB per octave drop off on either side) allows for earlier triggering in the eye movement.

Two op amps in the second TL074 each half wave rectify the output so that the output of each op amp is the filtered wave form for eye movements in one direction. The next wave form inverts one op amp's output and amplifies the two signals with a unit gain so that both directions of eye movements lead to signal deflections in the same direction. Thus, eye movements in either direction may cause triggers. The symmetry potentiometer is used to adjust the

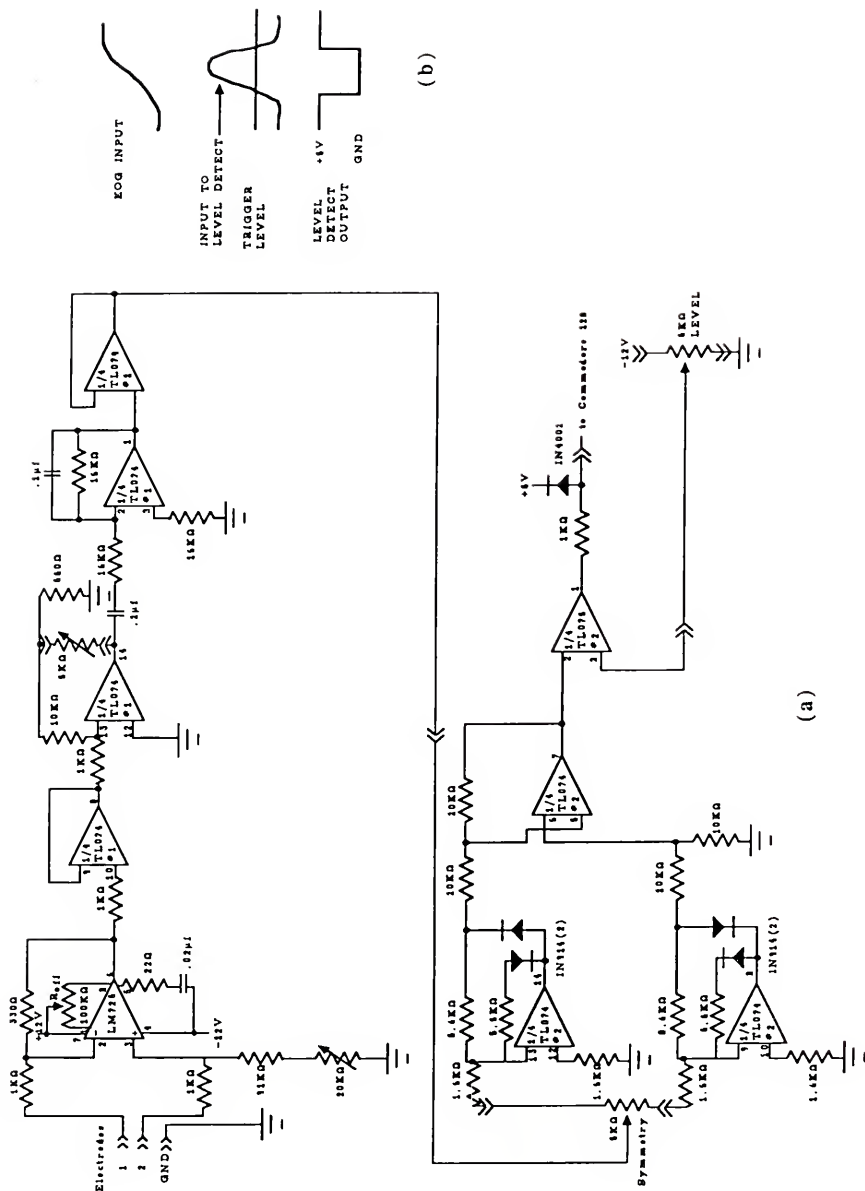


Figure A-1. EOG amplifier/trigger apparatus. a) Curcuit Diagram. b) Sample waveforms.

relative size of the wave forms in either direction so that any asymmetry in the EOG for eye movements in either direction can be corrected for on each subject. The final op amp is the level detector. When the input voltage raises above a certain level detection voltage, the output drops to 0 V as buffered on the output. This level detection voltage is adjustable via a third potentiometer.

APPENDIX B ASSEMBLY LANGUAGE ROUTINES USED IN EXPERIMENTS 1 AND 2

For every trial in Experiment 1, 5 machine language routines were called into operation. Their 8502 assembly language versions will be described in the sequence in which they were called by the main program. Address and machine language values are in hex.

1) INTRPT SETUP

<u>Address</u>	Machine	Assembly	<u>Comment</u>
	<u>Language</u>	<u>Language</u>	
1380	78	SEI	; Turn off machine interrupts.
1381	AD 14 03	LDA \$0314	; Store in memory locations 1806 and
1384	8D 06 18	STA \$1806	; 1807, the normal address of the IRQ
1387	AD 15 03	LDA \$0315	; vector (Locations 0314 and 0315).
138A	8D 07 18	STA \$1807	;
138D	A9 00	LDA #\$00	; Replace the IRQ vector with the
138F	8D 14 03	STA \$0314	; address 1300, the location of the
1392	A9 13	LDA #\$13	; programs own routine.
1394	8D 15 03	STA \$0315	;
1397	58	CLI	; restore normal IRQ operation
1398	60	RTS	; Return to BASIC program.

The function of this routine is to redirect the commodore IRQ interrupt (which occurs with every vertical refresh of the monitor screen) to a routine of the programs own choosing as a front end to the typical operations of the operating system. This routine is the only machine language routine that is not called by an interrupt. Thus, it ends with a return from subroutine to the Basic program.

2) HANDLER 1

<u>Address</u>	<u>Machine</u>	<u>Assembly</u>	<u>Comment</u>
	<u>Language</u>	<u>Language</u>	
1300	78	SEI	; Turn on IRQ interrupts.
1301	AE 09 18	LDX \$1809	; Load count of number of raster frames
1304	E8	INX	; since trial began and increment.
1305	EC 08 18	CPX \$1808	; Compare with value set for when
1308	F0 09	BEQ \$1313	; stimulus is to be presented.
130A	8E 09 18	STX \$1809	; If frame counts are equal jump to routine below to set up stimulus presentation.
130D	6C 06 18	JMP (\$1806);	Jump to normal routine called by IRQ
1310	EA	NOP	;
1311	EA	NOP	;
1312	EA	NOP	;
1313	A9 00	LDA #\$00	; Place location of routine to display
1315	8D 14 03	STA \$0314	; stimulus (\$1400) into IRQ indirect vector.
1318	A9 14	LDA #\$14	;
131A	8D 15 03	STA \$0314	;
131D	A9 33	LDA #\$33	; Place in raster interrupt location the
131F	8D 12 D0	STA \$D012	; raster line for interrupt to turn on stimulus.
1322	AD 1A D0	LDA \$D01A	; The rest of the routine sets up the
1325	09 01	ORA #\$01	; VIC video chip to allow for the
1327	8D 1A D0	STA \$D01A	; raster interrupt.
132A	AD 19 D0	LDA \$D019	;
132D	09 01	ORA #\$01	;
132F	8D 19 D0	STA \$D019	;
1332	AD 11 D0	LDA \$D011	;
1335	29 7F	AND #\$7F	;
1337	8D 11 D0	STA \$D011	;
133A	6C 06 18	JMP (\$1806);	Jump to routine to perform rest IRQ functions.

This routine serves two functions. First, it acts as a clock function counting video frames from the beginning of the trial to a predetermined value set for the target stimulus to be displayed. This counter is stored in \$1809 and will be continued to be incremented once per frame until a saccade is detected. The predetermined frame for the stimulus display is stored in \$1808. When these two values are equal, then the raster interrupt function on the video chip is set up to cause another IRQ at raster line 50 (hex 33). At this time

control is transferred to a routine at memory location \$1400, which is discussed next.

3) JUNK1

<u>Address</u>	<u>Machine</u>	<u>Assembly</u>	<u>Comment</u>
	<u>Language</u>	<u>Language</u>	
1400	AD 19 D0	LDA \$D019 ;	Clear the video interrupt flag so
1403	8D 19 D0	STA \$D019 ;	another IRQ can be processed.
1406	A9 FA	LDA #\$FA ;	Set next IRQ to occur at raster
1408	8D 12 D0	STA \$D012 ;	250 (hex FA) to remove stimulus
140B	A9 04	LDA #\$04 ;	Turn on sprite 4 (the stimulus).
140D	8D 15 D0	STA \$D015 ;	
1410	A9 15	LDA #\$15 ;	Set indirect IRQ vector to \$1500 for
1412	8D 15 03	STA \$0315 ;	next routine to remove stimulus.
1415	68	PLA ;	The remaining lines recover the
1416	8D 00 FF	STA \$FF00 ;	processor status that existed when
1419	68	PLA ;	the interrupt occurred, and then
141A	A8	TAY ;	returns from the interrupt.
141B	68	PLA ;	(There is a jump vector that has
141C	AA	TAX ;	these statements already laid out).
141D	68	PLA ;	
141E	40	RTI ;	

This routine will turn on the target stimulus (defined as sprite 3, but addressed in the third bit of \$D015 thus hex 04) and positioned by the basic program but left off. The target stimulus will begin to be displayed when the raster reaches raster line 150. In addition, the routine sets the computer to cause another IRQ to occur on raster line 250 of the same frame so that the target stimulus can be turned off. This routine is positioned in memory starting at address \$1500.

4) JUNK3

<u>Address</u>	<u>Machine</u>	<u>Assembly</u>	<u>Comment</u>
	<u>Language</u>	<u>Language</u>	
1500	A9 00	LDA #\$00 ;	Turn off the stimulus
1502	8D 15 D0	STA \$D015 ;	
1505	AD 06 18	LDA \$1806 ;	Restore the initial IRQ indirect
1508	8D 14 03	STA \$0314 ;	vector for future system IRQ's.
150B	AD 07 18	LDA \$1807 ;	


```

150E      8D 15 03      STA $0315 ;
1511      6C 14 03      JMP ($0314); Jump to the location now stored in
                                ; the IRQ indirect vector.

```

This routine will remove the target stimulus in the same frame as the target stimulus was displayed. Then the normal IRQ indirect vector is restored and the routine in this location is jumped to for normal operating system processing. The last routine used in Experiment 1 is called by 8502 NMI interrupts ("non maskable interrupts"), which registers when a saccade is detected by the amplifier/trigger apparatus which enters on the external NMI pin.

5)EYE MOVE

<u>Address</u>	<u>Machine</u>	<u>Assembly</u>	<u>Comment</u>
	<u>Language</u>	<u>Language</u>	
1480	AD 12 D0	LDA \$D012 ;	Store in memory the raster line and
1483	AE 09 18	LDX \$1809 ;	frame number from the offset of
1486	8D 0A 18	STA \$180A ;	initial stimuli during which the
1489	8E 0B 18	STX \$180B ;	NMI occurred.
148C	A9 65	LDA #\$65 ;	Store in \$1806 and 1807 the address of
148E	8D 06 18	STA \$1806 ;	the normal IRQ routine.
1491	A9 FA	LDA #\$FA ;	
1493	8D 07 18	STA \$1807 ;	
1496	68	PLA ;	The remaining lines recover the
1497	8D 00 FF	STA \$FF00 ;	processor status that existed when
149A	68	PLA ;	the interrupt occurred, and then
149B	A8	TAY ;	returns from the interrupt.
149C	68	PLA ;	(there is a jump vector that has
149D	AA	TAX ;	these statements already laid out).
149E	68	PLA ;	
149F	58	CLI ;	
14A0	40	RTI ;	

This routine will store in memory the raster line and the frame count from the beginning of the trial during which the NMI associated with the eye movement occurred. These values used in conjunction with the raster line and frame count from the onset of the probe stimulus will allow the computation of the relative time of occurrence of saccade onset and probe stimulus. The routine Handler 1 will continue to be called even after the probe stimulus is

called if an eye movement has not occurred. This is accomplished by the values in \$1806 and \$1807 containing the address of Handler 1. Thus if the eye movement occurs after the probe stimulus Handler 1 will still time. Once the eye movement occurs, the address in \$1806 and \$1807 are changed such that the normal sequence of events during a system IRQ are executed.

The next routine is used, in part, to control the sequence of events during Experiment 2.

1) GRAPHCLR

<u>Address</u>	<u>Machine</u>	<u>Assembly</u>	<u>Comment</u>
	<u>Language</u>	<u>Language</u>	
1300	A9 40	LDA #\$40	; Change memory banks.
1302	8D 00 D5	STA \$D500	; At this point the routine in the ; upper bank of memory is executed.
1305	A9 10	LDA #\$10	; Load into the accumulator the code ; for the foreground and background ; colors (white and black, ; respectively).
1307	A2 00	LDX #\$00	; Clear the x register.
1309	9D 00 1C	STA \$1C00,X	; Store the color codes in the the next ; memory location in the color ; memory.
130C	E8	INX	; Increment the x register.
130D	D0 FA	BNE \$1309	; Repeat until the x register returns to ; 0.
130F	AC 0B 13	LDY \$130B	; Change the value in memory location
1312	C8	INY	; 130B to set the next part of the color
1313	8C 0B 13	STY \$130B	; memory.
1316	C0 20	CPY #\$20	; The color memory is cleared when
1318	D0 ED	BNE \$1307	; \$130B contains \$20.
131A	A0 1C	LDY #\$1C	; Restore 130B to its initial state.
131C	8C 0B 13	STY \$130B	
131F	60	RTS	; Return to the basic program.

This routine prepares the graphics memory location that will contain the moving grating image in the upper bank of RAM memory of the Commodore 128 memory. This function would normally be accomplished by the GRAPHIC 1,1 command, but this command apparently does not work for other than the default graphic memory locations. This routine needs to be loaded into both

banks of memory. When the banks are changed to set up the upper bank screen memory, the computer will hang up if the routine is not present in the upper bank as well.

APPENDIX C
MODIFIED MACHINE LANGUAGE ROUTINES
USED WITH PSS TO RECORD AND TRIGGER OFF
OF THE EOG

To use the PSS system described by Shuman (in press) for Experiment 3, the machine language routines run by the data acquisition subsystem (DAS) and stimulus control subsystem (SCS) had to be modified. It should be noted, that the SCS and DAS software, while not new, are not the same software used by Shuman (in press). This software functions presents series of discrete stimulus motions specified by data statements with the SCS software. The timing between the stimulus motions are also specified within the SCS software.

The new functions of the PSS were to allow trigger pulses derived from the electrooculogram (EOG) to cause the beginning of a stimulus motion and to record at what point in the trial that the trigger occurred. Descriptively, the EOG derived trigger pulse was input to the SCS challenger. When the SCS detected a trigger, it signalled the DAS challenger which recorded which sample had last been collected. After the trial was over, the machine language routine sends the trigger information to the DPS for storage and later usage in the response averaging used in Experiment 3. Three other general features of the software need to be noted.

First, the DAS and DPS software are structured to receive any number of saccade triggers that occur. Only the SCS software needs to be set for the intended number of saccades in the trial. The DPS routine is structured to wait

for a time gap in the data transmission, and the DAS routine simply waits for the trigger signal from the SCS. In this way missed triggers will not affect the software of either the DAS or DPS.

Second, is that the routine in the SCS software can be entered in several locations. This fact is important because it can lead to different operations of the PSS system. For example, entering at the start is used for triggering stimulus motions off of saccades. Entering after the wait segment of the routine allows it to not trigger off of saccades, but to signal the DAS challenger that a stimulus motion will occur and cause the SPS to execute that motion. Entering after the part of the routine that signals the DAS challenger will cause stimulus motion but not signal the DAS challenger. This operation would be identical to how PSS was configured in Krantz and White (in preparation).

Last, a trigger pulse from the EOG will have no effect on the SCS system until the machine language routine is entered. Thus, careful entering of the routine can drastically reduce the effects of false triggers, but if the subject anticipates the saccade target, a saccade can be missed and the software hung up. Though in practice there was little problem with subjects anticipating the saccade target, so the EOG trigger apparatus could be set to be very sensitive.

In the following paragraphs, the specifics of the machine language routines will be presented highlighting those portions that are new. Both routines are written in 6502 machine language (the assembly codes are also provided), and implemented on Challenger 1P's.

In the SCS machine language routine, called SACMLP, a wait routine was added to the beginning. When a bit on an input pin went low, another bit on the same port configured as an output line was toggled from its previous state,

that is, if it is high it was set low, if it was low it was set high. By convention both machines started trials with this pin high.

1) SACMLP

LINE	ADDRESS	MACHINE LANGUAGE	ASSEMBLY LANGUAGE	COMMENTS
10	1900		*=\$1900	; SACMLP: 1-SEPT-87
20	1900		DELAY=\$1960	; Stimulus motion control
				; Location of time between
				; updates to SCS D/A
				; converter
30	1900	A9 01	LDA#\$01	; Wait until bit 0 on I/O port
40	1902	2C 01 20	WAIT BIT \$2001	; at location \$2001 goes low.
50	1905	DOFB	BNE WAIT	;
60	1907	A9 02	LDA #\$02	; Load a 1 in to bit one of the
70	1909	4D 50 19	EOR \$1950	; accumulator, then
85	190C	8D 01 20	STORE STA \$2001	; exclusive or with current
				; contents of \$1950. This
				; operation alternates the
				; value of this bit. Then
				; send this toggled value
				; to the DAS challenger.
90	190F	8D 50 19	STA \$1950	; Replace old value in \$1950
				; with toggled value.
100	1912	A9 00	LDA #\$00	; The remainder of the
110	1914	BD 00 1A	LDX #\$00	; routine is the same as
120	1916	BD 00 1A	AGAIN LDA \$1A00,X	; used by Krantz and White
130	1919	8D 00 20	STA \$2000	; (in preparation). Some
140	191C	A9 FF	LDA #\$FF	; values in this routine are
150	191E	8D 0A 20	STA \$200A	; changed by the basic
160	1921	AD FF	LDY #\$FF	; program before it is
170	1923	C8	INY	; called.
180	1924	EA	NOP	;
190	1925	BD 01 1A	LDA \$1A01,X	;
200	1928	8D 00 20	STA \$2000	;
210	192B	E8	INX	;
220	192C	E8	INX	;
230	192D	A9 00	LDA #\$00	;
240	192F	8D 0A 20	STA \$200A	;
250	1932	88	BACK DEY	;
260	1933	D0 39	BNE DELAY	;
270	1935	C6 E0	DEC \$E0	;
280	1937	D0 221	BNE AGAIN	;
290	1939	6C 08 00	JMP (\$0008)	;

If the machine language routine is entered at the beginning, the routine waits until bit 0 of VIA #1 goes low. Then a value in memory location \$1950 is read,

and bit one is toggled by an exclusive-or with a 1 in bit 1. This new value on bit 1 is sent to the DAS challenger via line 1 of the same VIA.

2) TWOMLP

LINE	ADDRESS	MACHINE LANGUAGE	ASSEMBLY LANGUAGE	COMMENTS
10	1EA4		*=\$1EA4	; TWOMLP 1-OCT-87
				; Data Acquisition
				; Subsystem with trigger.
20	1EA4	A9 00	BEGIN LDA #\$00	;
30	1EA6	85 E7	STA \$E7	;
40	1EA8	AA	TAX	;
50	1EA9	A8	TAY	;
60	1EAA	A9F0	LDA #\$F0	;
70	1EAC	8D 4F 1F	STA \$1F4F	;
80	1EAF	8D BB 1F	STA \$1FBB	;
90	1EB2	8D C4 1F	STA \$1FC4	;
100	1EB5	A9 FF	START LDA #\$FF	;
110	1EB7	8D 08 78	STA \$7808	;
120	1EBA	8D 09 78	STA \$7809	;
130	1EBD	A9 08	LDA #\$08	;
140	1EBF	2C 00 28	BIT \$2800	;
150	1EC2	F0 0C	BEQ SWITCH	;
160	1EC4	A5 F2	LDA \$F2	;
170	1EC6	C5 F4	CMP \$F5	;
180	1EC8	D0 33	BNE NOSW	;
190	1ECA	A5 F3	LDA \$F3	;
200	1ECC	C5 F5	CMP \$F5	;
210	1ECE	D0 2D	BNE NOSW	;
220	1ED0	A9 02	SWITCH LDA #\$02	;
230	1ED2	2C 00 F0	FILL BIT \$F000	;
240	1ED5	F0 FB	BEQ FILL	;
250	1ED7	A9 FF	LDA #FF	;
260	1ED9	8D 01 F0	STA \$F001	;
270	1EDC	C8	INY	;
280	1EDD	C0 08	CPY #\$08	;
290	1E DF	D0 EF	BNE SWITCH	;
291	1EE1	A0 00	LDY #\$00	; After the final position
292	1EE3	A9 02	SACTM LDA #\$02	; has been sent to the
293	1EE5	2C 00 F0	FILLD BIT \$F000	; DPS computer, the
294	1EE8	F0 FB	BEQ FILLD	; samples during which
295	1EEA	B9 6C 1B	LDA \$1B6C,Y	; saccades were detected
296	1EED	8D 01 F0	STA \$F001	; are also sent to DPS. The
297	1EF0	C8	INY	; number of saccades are
298	1EF1	CC 63 1B	CPY \$1B63	; stored online in \$1B63 and
299	1EF4	D0 ED	BNE SACTM	; samples times are store at
				; and following \$1B6C.
300	1EF6	A4 F2	LDY \$F2	; Normal routine exit.
310	1EF8	A5 F3	LDA \$F3	;
320	1EFA	6C 08 00	JMP (\$0008)	;

330	1EFD	A9 01	NOSW LDA #\$01	;	
340	1EFF	2C 00 28	AGAIN BIT \$2800	;	
350	1F02	F0 FB	BEQ AGAIN	;	
360	1F04	A9 02	LDA \$02	;	Check to see if the saccade
370	1F06	2D 01 30	AND \$3001	;	pin has toggled.
375	1F09	4D 62 1B	EOR \$1B62	;	
380	1F0C	F0 21	BEQ INCR	;	If not jump to INCR.
383	1F0E	A9 02	LDA #\$02	;	If so store the new value of
385	1F10	4D 62 1B	EOR \$1B62	;	the saccade pin in \$1B62
393	1F13	8D 62 1B	STA \$1B62	;	
400	1F16	8E 64 1B	STX \$1B64	;	Hold current X register
				;	value to restore later.
405	1F19	AE 63 1B	LDX \$1B63	;	Load in the X register the
				;	number of saccades
				;	received so far.
410	1F1C	A5 F2	LDA \$F2	;	Load in the next position
420	1F1E	9D 6C 1B	STA \$1B6C,X	;	following 1B6C the
430	1F21	A5 F3	LDA \$F3	;	number of the sample
440	1F23	9D 6D 1B	STA 1B6D,X	;	most recently collected.
				;	Thus, 1B6C forms a table
				;	of saccade times.
450	1F26	EE 63 1B	INC \$1B63	;	Increment the saccade
455	1F29	EE 63 1B	INC \$1B63	;	counter by 2 since 2
				;	bytes are necessary to
				;	store the sample number.
				;	Resume normal routine
460	1F2F	E6 F2	INCR INC \$F2	;	flow.
470	1F31	D0 02	BNE CLEAR	;	
480	1F33	E6 F3	INC \$F3	;	
490	1F35	A9 01	CLEAR LDA #\$01	;	
500	1F37	8D 00 28	STA \$2800	;	
510	1F3A	A9 05	LDA #\$05	;	
520	1F37	8D 00 28	STA \$2800	;	
530	1F3F	8A	TXA	;	
540	1F40	F0 05	BEQ TRANS	;	
550	1F42	A9 F8	LDA #\$F8	;	
560	1F44	8D 4F 1F	STA \$1F4F	;	
570	1F47	A9 02	TRANS LDA #\$02	;	
580	1F49	2C 00 F0	FULL BIT \$F000	;	
590	1F4C	F0 FB	BEQ FULL	;	
600	1F4E	B9 F0 1F	LDA \$F001,Y	;	
610	1F51	8D 01 F0	STA \$F001	;	
620	1F54	C8	INY	;	
630	1F55	C0 08	CPY #\$08	;	
640	1F57	D0 EE	BNE TRANS	;	
650	1F59	A0 00	LDY #\$00	;	
660	1F5B	8A	TXA	;	
670	1F5C	D0 23	BNE CLICK	;	
680	1F5E	AD 00 28	LDA \$2800	;	
690	1F61	4A	LSR A	;	
700	1F62	45 E7	EOR 4E7	;	
710	1F64	29 01	AND #\$01	;	
720	1F66	D0 44	BNE READ	;	
730	1F68	EE BA D3	INC 54202	;	
740	1F68	A9 3A	LDA #\$3A	;	

750	1F6D	CD BA D3	CMP 54202	;
760	1F70	D0 08	BNE LESS9	;
770	1F72	A9 30	LDA #\$30	;
780	1F74	8D BA D3	STA 54202	;
790	1F77	EE B9 D3	STA 54201	;
800	1F7A	AE 4F 1F	LESS9 LDX \$1F4F	;
810	1F7D	E0 F0	CPX #\$F0	;
820	1F7F	F0 60	BEQ TRAP	;
830	1F81	A9 01	CLICK LDA #\$01	;
840	1F83	2C 00 28	WAIT BIT \$2800	;
850	1F86	F0 FB	BEQ WAIT	;
860	1F88	A9 00	LDA #\$00	;
870	1F8A	99 F0 1F	STUFF STA \$1FF0,Y	;
880	1F8D	C8	INY	;
890	1F8E	C0 10	CPY #\$10	;
900	1F90	D0 F8	BNE STUFF	;
910	1F92	A8	TAY	;
920	1F93	A9 01	LDA #\$01	;
930	1F95	2C 00 28	WAIT1 BIT \$2800	;
940	1F98	D0 FB	BNE WAIT1	;
950	1F9A	2C 00 30	WAIT2 BIT \$3000	;
960	1F9D	D0 FB	BNE WAIT2	;
970	1F9F	2C 00 48	WAIT3 BIT \$4800	;
980	1FA2	D0 FB	BNE WAIT3	;
990	1FA4	2C 00 50	WAIT4 BIT \$5000	;
1000	1FA7	D0 FB	BNE WAIT4	;
1010	1FA9	4C A4 1E	JMP BEGIN	;
1020	1FAC	B9 E8 00	READ LDA \$E8,Y	;
1030	1FAF	8D B7 1F	STA \$1FB7	;
1040	1FB2	8D C0 1F	STA \$1FC0	;
1050	1FB5	AD 08 28	LDA \$2808	;
1060	1FB8	49 FF	EOR #\$FF	;
1070	1FBA	99 F0 1F	STA \$1FF0,Y	;
1080	1FBD	C8	INY	;
1090	1FBE	AD 09 28	LDA \$2809	;
1100	1FC1	49 FF	EOR #\$FF	;
1110	1FC3	99 F0 1F	STA \$1FF0,Y	;
1120	1FC6	C8	INY	;
1130	1FC7	C0 80	CPY #\$08	;
1140	1FC9	D0 E1	BNE READ	;
1150	1FCB	A0 00	LDY #\$00	;
1160	1FCD	AD 4F 1F	LDA \$1F4F	;
1170	1F D0	69 07	ADC #\$07	;
1180	1FD2	D0 02	BNE NEXTSP	;
1190	1FD4	A9 F0	LDA #\$F0	;
1200	1FD6	8D 4F 1F	NEXTSP STA \$1F4F	;
1210	1FD9	8D BB 1F	STA \$1FBB	;
1220	1FDC	8D C4 1F	STA \$1FC4	;
1230	1FDF	E6 E7	INC \$E7	;
1240	1FE1	A9 01	TRAP LDA #\$01	;
1250	1FE3	2C 00 28	BIT \$2800	;
1260	1FE6	D0 03	BNE FAST	;
1270	1FE8	4C B5 1E	JMP START	;
1280	1FEB	A9 FF	FAST LDA #\$FF	;

```
1290 IFED      6C 08 00    JMP ($0008)      ; Return to the basic  
                                           ; program.
```

When the second pin on variable interface adaptor 2 toggles, this routine records the sample that has most recently be collected. These data are stored in the form of a saccade trigger table that is sent down the serial interface to the DPS before the routine is exited. The number of saccades in the table are collected online so that only the SCS software needs to be changed for different numbers of saccades in a trial. Other than the areas indicated, the software operates in the same manner as used by Krantz (1985).

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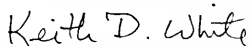
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BIOGRAPHICAL SKETCH

John Krantz was born in Columbus, Ohio, on February 18, 1960. Not much of interest, even to him, happened until he went to St. Andrews Presbyterian College where he found his love in studying the human visual system. After St. Andrews he proceeded to the University of Florida where he first obtained his master's degree and now his Ph.D. finding out about eyeballs. Over the years, the visual system has only become more, not less, fascinating.

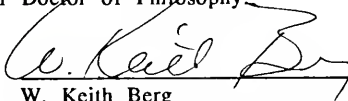
Other items of interest, at least to him, are that during his stay he met his wonderful wife, and both had their first child, Michael, a source of great joy. John is now employed, at least temporarily, by Honeywell in an attempt to put what he has learned to use (a novel idea). During this sojourn in the frozen north (Minneapolis, Minnesota), John and Margaret's second child Jennifer has been born. Will Michael be able to stand it?

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



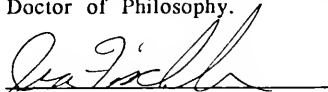
Keith D. White, Chair
Associate Professor of Psychology

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W. Keith Berg
Associate Professor of Psychology

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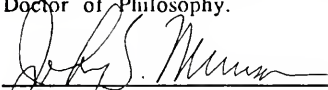
Ira Fischler
Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



David M. Green
Graduate Research Professor
of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



John Munson
Professor of Neuroscience

This dissertation was submitted to the Graduate Faculty of the Department of Psychology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

April, 1988

Dean, Graduate School

